

**Abstract**—The *Caranx hippos* species complex comprises three extant species: crevalle jack (*Caranx hippos*) (Linnaeus, 1766) from both the western and eastern Atlantic oceans; Pacific crevalle jack (*Caranx caninus*) Günther, 1868 from the eastern Pacific Ocean; and longfin crevalle jack (*Caranx fischeri*) new species, from the eastern Atlantic, including the Mediterranean Sea and Ascension Island. Adults of all three species are superficially similar with a black blotch on the lower half of the pectoral fin, a black spot on the upper margin of opercle, one or two pairs of enlarged symphyseal canines on the lower jaw, and a similar pattern of breast squamation. Each species has a different pattern of hyperostotic bone development and anal-fin color. The two sympatric eastern Atlantic species also differ from each other in number of dorsal- and anal-fin rays, and in large adults of *C. fischeri* the lobes of these fins are longer and the body is deeper. *Caranx hippos* from opposite sides of the Atlantic are virtually indistinguishable externally but differ consistently in the expression of hyperostosis of the first dorsal-fin pterygiophore. The fossil species *Caranx carangopsis* Steindachner 1859 appears to have been based on composite material of *Trachurus* sp. and a fourth species of the *Caranx hippos* complex. Patterns of hyperostotic bone development are compared in the nine (of 15 total) species of *Caranx sensu stricto* that exhibit hyperostosis.

## Review of the crevalle jacks, *Caranx hippos* complex (Teleostei: Carangidae), with a description of a new species from West Africa

William F. Smith-Vaniz (contact author)<sup>1</sup>

Kent E. Carpenter<sup>2</sup>

Email address for W. F. Smith-Vaniz: bill\_smith-vaniz@usgs.gov

<sup>1</sup> U.S. Geological Survey

7920 NW 71st Street

Gainesville, Florida 32653

Present address: Division of Ichthyology

Florida Museum of Natural History

Dickinson Hall, Museum Road

University of Florida

Gainesville, Florida 32611-7800

<sup>2</sup> Department of Biological Sciences

Old Dominion University

Norfolk, Virginia 23529

Species of the *Caranx hippos* complex or crevalle jacks (Fig. 1) are fished commercially or recreationally in coastal waters throughout their range. Recognized as “superb light tackle species” by the International Game Fish Association (IGFA, 2006), they are important apex predators in inshore tropical waters—all species attaining maximum sizes approaching or exceeding 22.7 kg (50 lb). They are also commonly exhibited in public aquaria and books on marine fishes usually include accounts of them for the areas where these species are found. Despite this importance, there has been considerable confusion regarding the taxonomy and geographic distributions of these species. Gill and Kemp (2002) discussed the potentially serious implications for fishery and conservation managers of an inadequate taxonomic understanding of putatively widespread shore-fish species. Blaber (2002) noted that one of the major obstacles to ecological research in developing countries is the difficulty associated with correct identification of tropical marine and estuarine fishes, which is exacerbated by an overall decline in funding throughout the world for taxonomic research.

In a general review of the phenomenon of hyperostosis in fishes, including those of the allopatrically distributed and externally nearly identical species *Caranx hippos* (Linnaeus) (Atlantic Ocean) and *C. caninus* Günther (eastern Pacific Ocean), Smith-Vaniz et al. (1995) determined that patterns of hyperostotic bone development were often species-specific. These findings stimulated us to re-evaluate the taxonomic status of specimens from the eastern Atlantic identified as *Caranx hippos*, which we herein recognize as actually representing two species. The primary objectives of this research were to describe a new species of West African *Caranx* that has been routinely misidentified as *C. hippos*, to provide diagnoses and comparisons for all members of the *Caranx hippos* complex, and to determine their geographic distributions.

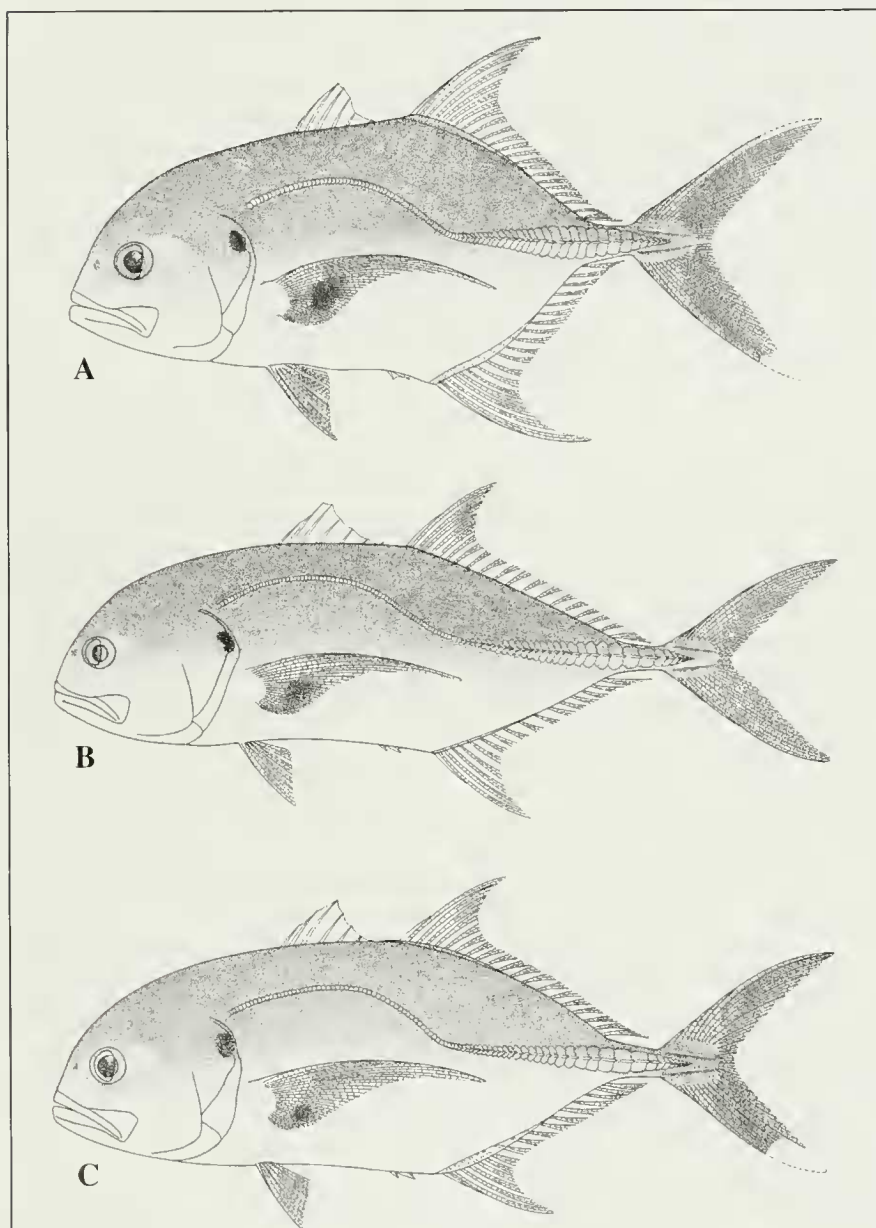
This study has been hampered by the scarcity of preserved adults of *Caranx hippos* from the eastern Atlantic. This scarcity is not surprising because natural history museums and institutional fish collections do not exist in any coastal West African country, and preservation and shipment of large fish specimens from the region

are logistically difficult. Color photographs of *Caranx hippos* provided by the International Game Fish Association and numerous colleagues indicate that adults of this species are relatively common locally, especially during October to February. We urge fishery biologists and others who have the opportunity to obtain adults of fishes that mature at relatively large sizes to help ensure that at least a few such specimens are available in major research collections.

### Taxonomic history

The genus *Caranx* was established by Lacépède (1801, p. 57) and the type-species *Caranx carangua* Lacépède was apparently first designated by Desmarest (1856, p. 242) as *Caranx carougu* [sic] Bloch, which is a junior synonym of *Scomber hippos* Linnaeus. Two other generic or subgeneric names have been applied to these species (*Tricropterus* Rafinesque, 1810 and *Carangus* Girard, 1858), but both are junior synonyms of *Caranx* because the type species of these nominal taxa is also *Scomber carangus* Bloch.

*Caranx hippos* was first described (Linnaeus, 1766) from Carolina as *Scomber hippos*. The putative holotype, a right half-skin (Wheeler, 1985), was included in one of the last shipments of dried fish specimens sent to Linnaeus by the colonial physician Alexander Garden (Sanders, 1997). Synonyms of *Caranx hippos* (see species account) are either unnecessary replacement names or Linnaeus's original description was not considered. Nichols (1920), because his superficial description of his new Brazilian subspecies, *Caranx hippos tropicus*, was based on too few specimens, failed to appreciate the range of variation in the species, and other workers have correctly disregarded this trinomial. In his description of the eastern Pacific *Caranx caninus*, Gunther (1867, 1868) did not compare this species with any other species. Jordan and Gilbert (1883), Jordan (1895), and Gilbert and Starks (1904) all concluded that this nominal species was indistinguishable from the western Atlantic *C. hippos*. In their major work on the fishes of Panama, Meek and Hildebrand (1925) also did not recognize *C. caninus* as a valid species, stating "a careful comparison of our large series from the two coasts discloses no differences of importance." Hildebrand (1946) continued to recognize fish from both oceans as conspecific. Berry (1974) stated that eastern Pacific and western Atlantic specimens of *Caranx hippos* are essentially identical. Eschmeyer and Herald (1983) stated that *C. caninus* might not be a valid species. Eschmeyer (1998)



**Figure 1**

The *Caranx hippos* species complex: (A) longfin crevalle jack (*C. fischeri*), 358 mm FL, BMNH 1927.12.7.49, Ascension Island; (B) crevalle jack (*C. hippos*), 390 mm FL, USNM 33247, Florida, Dixie Co., Swannee River; (C) Pacific crevalle jack (*C. caninus*), 359 mm FL, USNM 127918, Peru, Lobos de Tierra Island. Illustrations by Tracy D. Pedersen.



and Castro-Aguirre et al. (1999) both treated it as a synonym of *C. hippos*; however, the former subsequently recognized *C. caninus* as a valid species (Eschmeyer<sup>1</sup>).

Most recent authors have recognized a single eastern Atlantic member of this species group, which has been uncritically referred to as *Caranx hippos* (Fowler, 1936; Bini, 1968; Hureau and Tortonese, 1973; Bauchot and Pras, 1980; Smith-Vaniz and Berry, 1981; Smith-Vaniz, 1986; Smith-Vaniz et al., 1990; Bauchot, 1992). In the few cases where two species were recognized (Cadenat, 1960; Blache et al., 1970; Okera, 1978), the scientific names used for both species were misapplied. The name *C. carangus* Valenciennes [sic] (the account given in Cuvier and Valenciennes, 1833 is not an original description) was used for the true *C. hippos* and the superficially similar new species (*C. fischeri*) was routinely misidentified as *C. hippos*.

## Materials and methods

Abbreviations used for institutional depositories and cooperative organizations are as follows: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); The Natural History Museum, London (BMNH); California Academy of Natural Sciences, San Francisco (CAS, CAS-SU); Food and Agricultural Organization of the United Nations, Rome (FAO); International Game Fish Association, Dania Beach, Florida (IGFA); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB); Musée Royal des de l'Afrique Centrale, Tervuren (MRAC); Museum National d'Histoire Naturelle, Paris (MNHN); Naturhistorisches Museum, Wien (Vienna), Austria (NMW); South African Institute of Aquatic Biodiversity (formerly J. L. B. Smith Institute of Ichthyology), Grahamstown (SAIAB); Scripps Institution of Oceanography, La Jolla (SIO); Florida Museum of Natural History, Gainesville (UF); National Museum of Natural History, Washington, D. C. (USNM); Universität Hamburg (ISH, ZMH); Zoological Museum, University of Copenhagen (ZMUC).

Parenthetical expressions in material examined include number of specimens, if more than one, followed by the size range in millimeters fork length (FL); cleared and stained specimens are indicated as "C&S." Localities are abbreviated and listed only by major geographic areas for *Caranx caninus* and western Atlantic *C. hippos*. Except for those given in the scatter plots, measurements are of limited value in distinguishing members of the *hippos* complex (and then only for specimens >200 mm FL). Total lengths (TL) are given when that was the only length measurement reported in cited references. All measurements are in mm unless specified as cm. Measurements expressed

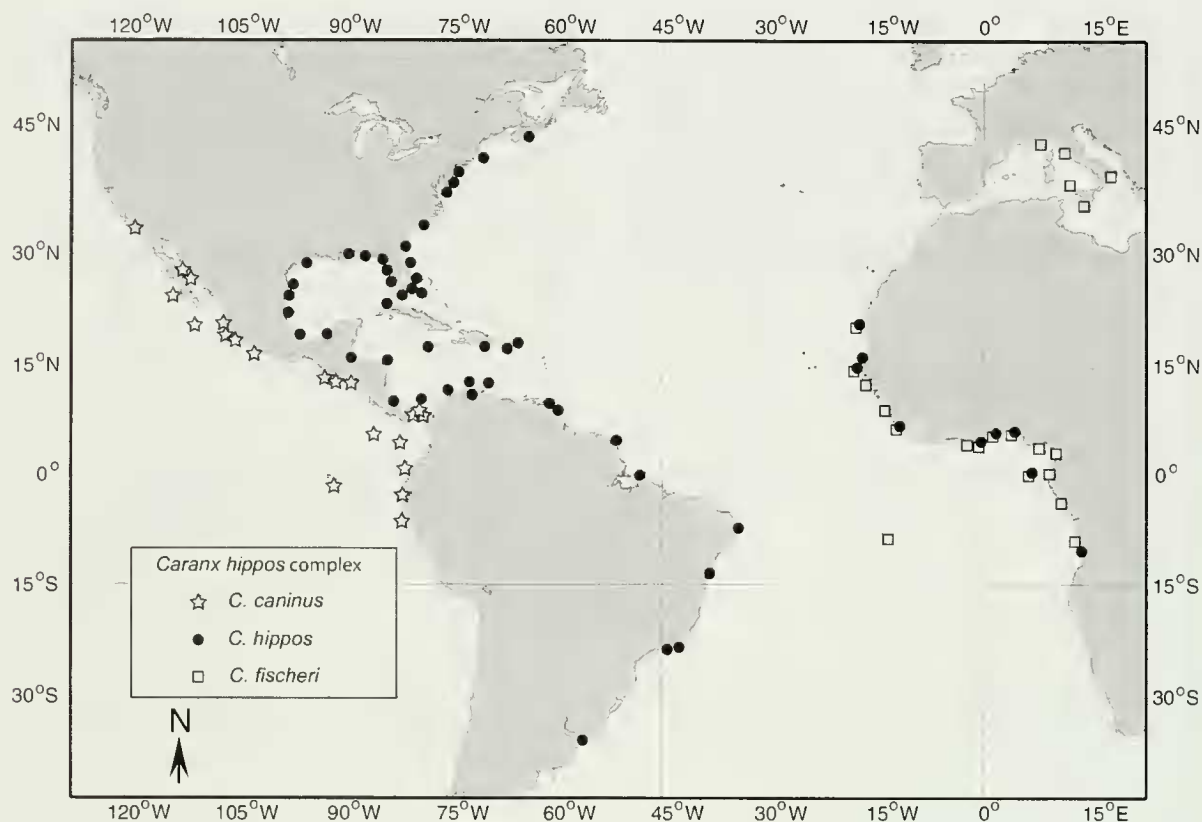
in percent fork length or head length, are given only in the description of the new species *Caranx fischeri*. Fork length is measured from the front of the upper lip to the tip of shortest median caudal-fin ray. Body depths are measured from the anterior base of the spinous dorsal fin (D10) to the origin of the pelvic fin (P20) and from the anterior base of the spine at the origin of the dorsal-fin lobe (D20) to the anterior base of the anal-fin spine at the origin of the anal-fin lobe (A20). Lengths of the dorsal- (D2) and anal-fin (A2) bases are straight-line measurements from either the D20 or A20 to the posterior base of the terminal fin ray of the respective fin. Head length is measured from the front of the upper lip to the posterior end of the opercular flap. Snout length is measured from the anterior end of the upper lip to the anterior edge of the eye. Eye diameter is the greatest bony diameter. Upper jaw length is taken from the anterior end of the upper lip to the posterior end of the maxilla. The curved part of the lateral line is measured as a chord (straight-line distance) of the arch extending from the upper edge of the opercle to its junction with the straight part; the straight part of the lateral line is measured from its junction with the curved part to its termination on the caudal-fin base (end of last scute). Scutes are defined as scales that have a raised horizontal ridge or a small to moderate projecting spine on the posterior margin ending in a point not exceeding a 120° angle; for detailed description and illustrations of scute formation and development in *Caranx crysos* (Mitchill) see Berry (1960). All scutes were counted, including those extending onto the caudal-fin base. Pectoral-fin ray counts do not include the dorsal-most spine-like element. Gill raker counts are from the first gill arch (usually on the right side), and the raker at the angle is included in the lower-limb count; rudimentary gill rakers, with the diameter of their bases greater than their height, are defined as tubercles or short rakers. The anterior dorsal-fin pterygiophore formula indicates the interdigitation pattern of supraneurals and pterygiophores within interneural spaces; neural spines are indicated by slashes, supraneural (predorsal) bones by an "S," pterygiophores by "2" (pterygiophores with two supernumerary rays and a serially associated ray) or "1" (no supernumerary ray and one serially associated ray).

## Results

### Taxonomy and distributions

Some recent authors (Amezcuca-Linares, 1996; Randall, 1996; McBride and McKown, 2000) still follow Briggs (1960) in erroneously reporting a worldwide distribution in tropical and subtropical latitudes for *Caranx hippos*, although Nichols (1920) had correctly concluded that records of the species from the Indian and western Pacific oceans were based on misidentifications. Other authors (Talwar and Kacker, 1984; Krishnan and Mishra, 1994; Mishra et al., 1999; Khan, 2003;

<sup>1</sup> Eschmeyer, W. N. Catalog of fishes, on-line edition. Website: <http://www.calacademy.org/research/ichthyology/catalog/> (accessed June 2006).



**Figure 2**

Distribution of members of the crevalle jack (*Caranx hippos*) complex: (Mediterranean locality records for longfin crevalle jack (*C. fischeri*) are based solely on literature reports; discussion of geographic distribution appears in individual species accounts).

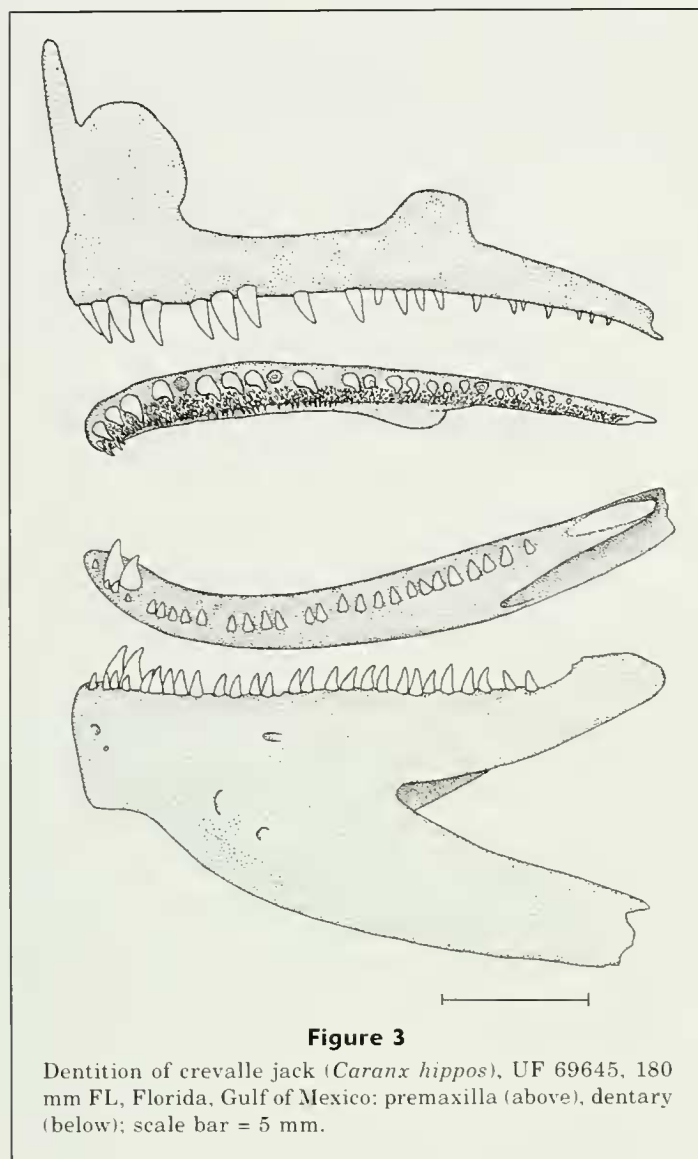
Mishra and Krishnan, 2003) reported *C. hippos* as *C. carangus* (Bloch) from the Indian Ocean based on misidentifications of *Caranx heberi* (Bennett). What was once considered to be a single widespread species is herein recognized as consisting of three species (Fig. 2). For almost a century, most ichthyologists and fishery biologists who have worked on West African crevalle jacks have failed to distinguish the new species *Caranx fischeri* described herein from *C. hippos*, although both species are commonly taken together.

Adults of *Caranx hippos* from opposite sides of the Atlantic Ocean are indistinguishable externally but exhibit consistent differences in the degree of development of the hyperostosis in the first dorsal-fin pterygiophore and neural spines of some of the anterior vertebrae (see "Geographic variation" in *C. hippos* species account). Although we consider these predictable ontogenetic and consistent site-specific patterns obvious evidence of genetic divergence associated with bone metabolism, an important consideration is the unknown functional significance of hyperostosis. In light of this, we believe it would be premature to recognize the eastern Atlantic population of *C. hippos* as taxonomically distinct. No formal change in classification should be made in the absence of collaborative molecular data.

### The *Caranx hippos* complex

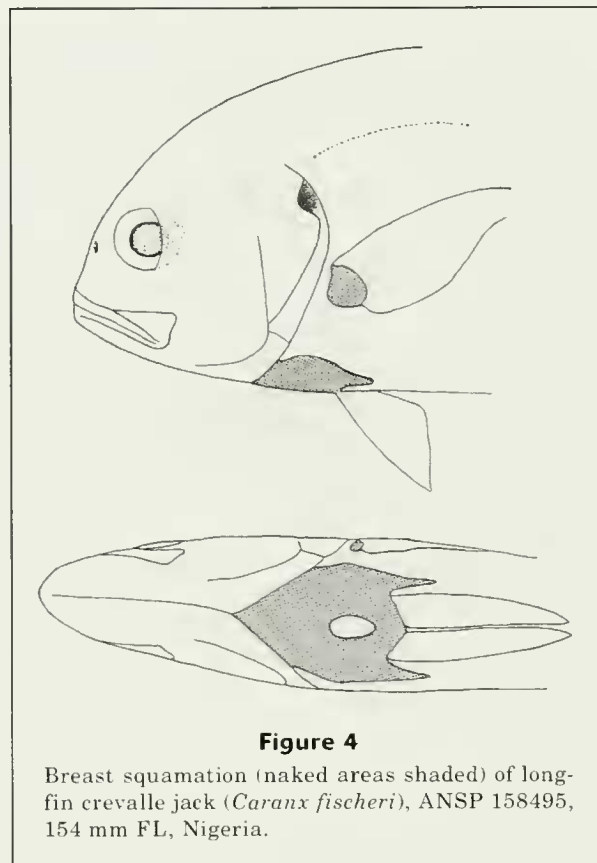
The *C. hippos* species complex can be diagnosed by the following combination of characters: a pair of strong symphyseal dentary canines (Fig. 3); breast naked ventrally except for a small oblong patch of prepelvic scales (Fig. 4) which forms at about 30 mm FL; rounded black blotch on the lower rays of the pectoral fin in adults; large black opercular spot; and vertebrae 10 precaudal + 14 caudal. Only the black blotch on the pectoral fin is unique to these species. Adults of the horse-eye jack, *Caranx latus* Agassiz, occasionally have a somewhat similarly placed dusky blotch on the pectoral fin (although the dark area is different in character and never as well defined as in *C. hippos*), and this similarity in appearance has occasionally resulted in field misidentifications, especially by scuba divers unfamiliar with both species. The typical breast squamation pattern of the *C. hippos* species complex is not duplicated in any other Atlantic or eastern Pacific species of *Caranx*, although it occurs in three Indo-west Pacific species: commonly in *C. ignobilis* (Forsskål) and *C. papuensis* Alleyne and Macleay, and less frequently in *C. heberi*. Dentition has been used as an important diagnostic character of carangid genera, but comparison of the dentition of a large number of





carangid species reveals an almost complete continuum of dentition types that in some cases does not agree with traditional generic assignments. In all members of the *C. hippos* complex the upper jaw has an outer row of strong canines (widely spaced in adults) and an inner band of small villiform teeth that is widest anteriorly. The lower jaw has a single row of strong conical teeth that are smaller anteriorly, and one or two pairs of noticeably enlarged inner symphyseal canines. Enlarged symphyseal dentary canines are absent in the following species of *Caranx*: *C. crysos*, *C. caballus* Günther, *C. melampygus* Cuvier, *C. papuensis*, and *C. senegallus* Cuvier. Gill (1862) proposed the genus *Paratractus* for *Caranx pisquetus* Cuvier, a junior synonym of *C. crysos*, primarily because of the absence of symphyseal canines.

Some recent authors follow Randall (1996) in assigning several common Atlantic carangids to the genus *Carangoides* Bleeker, but we maintain traditional usage for reasons given by Smith-Vaniz et al. (1999, p. 237).



#### Hyperostosis in *Caranx* species

Hyperostosis appears to have been an integral part of the evolutionary history of the *Caranx hippos* complex, but the pattern of expression is surprisingly different in each species (Table 1). Hyperostosis involves the expansion or swelling of certain bones into globose, gall-like structures characterized by cellular bone foci and bone-resorbing osteoclasts.

In most carangids the condition is usually apparent only in relatively large individuals (but can be detected histologically in smaller individuals) and the onset in different bone foci is typically sequential rather than simultaneous. A large number and size range of individuals of each species usually must be examined before the ontogenetic pattern can be precisely determined. Although Smith-Vaniz et al. (1995) were unable to determine the functional significance of hyperostosis, they found no histological evidence of hyperostosis as a pathologic condition and concluded that the intraspecific predictability and site-specificity of hyperostosis in a taxonomically diverse group of marine fishes was indicative of genetic control.

A detailed description of hyperostosis in *Caranx* is beyond the scope of this article, but to appreciate the context of its site-specificity and distribution in the *C. hippos* complex we briefly discuss its known occurrence in the genus. We found no evidence of hyperostosis in adults of six species: *C. heberi*, *C. ignobilis*, *C. lugubris*

Table 1

Comparison of hyperostosis in the *Caranx hippos* species complex. Sizes are minimum fork length at which hyperostosis is usually developed in all individuals.

| Hyperostotic bones                 | <i>C. fischeri</i><br>(E. Atlantic)                          | <i>C. hippos</i><br>(E. Atlantic) | <i>C. hippos</i><br>(W. Atlantic)                             | <i>C. caninus</i><br>(E. Pacific)                                |
|------------------------------------|--------------------------------------------------------------|-----------------------------------|---------------------------------------------------------------|------------------------------------------------------------------|
| Posttemporal                       | yes >20 cm, Fig. 5                                           | none                              | none                                                          | none                                                             |
| Cleithrum                          | none                                                         | well-developed, >35 cm<br>Fig. 10 | well-developed, >35 cm<br>Figs. 9, B–C                        | none                                                             |
| Neural spines                      | none                                                         | slight, 56 cm                     | well-developed, >40 cm<br>Figs. 9, B–C, 13                    | none                                                             |
| Pleural ribs                       | well-developed >34 cm<br>(usually ribs 5–7),<br>Figs. 5, B–C | slight, 56 cm<br>(ribs 6–8)       | well-developed, >38 cm<br>(usually ribs 6–8),<br>Figs. 9, B–C | none or 5th rib only,<br>Fig. 14A<br>(in 6 of 16 spec.<br>>34cm) |
| Pelvic girdle                      | none                                                         | well-developed, 56 cm             | well-developed, >50 cm                                        | well-developed, >45 cm                                           |
| 1st pterygiophore<br>of dorsal fin | none<br>Figs. 5, 11                                          | slight,<br>Figs. 10, 11, 12A      | well-developed,<br>Figs. 9, 11, 12B                           | well-developed,<br>Figs. 11, 14                                  |
| 1st pterygiophore<br>of anal fin   | none<br>not convex anteriorly<br>convex anteriorly,          | none<br>not convex anteriorly     | none<br>not convex anteriorly,<br>Fig. 15                     | well-developed,<br>>40 cm<br>Figs. 14, 15                        |

Poey, *C. melampygus*, *C. papuensis*, and *C. tille* Cuvier. In addition to *C. fischeri*, hyperostotic posttemporal bones are present in large individuals of the blue runner (*C. crysos*) and green jack (*C. caballus*) allopatric species that are possibly conspecific. *Caranx hippos* is exceptional in that the neural spines of at least vertebrae 6–12 are hyperostotic in large adults. The ventral end of the cleithrum is hyperossified in large *C. hippos*, *C. latus*, and *C. sexfasciatus*, but the shape of the hyperossification is noticeably different (wider and shorter) in the latter two species, which also differ from *C. hippos* in having two separate regions of hyperostosis on the cleithrum. The pelvic bones are hyperossified only in *C. hippos* and *C. caninus*. In large adults of *C. caninus* and western Atlantic *C. hippos* the first pterygiophore of the spinous dorsal fin becomes so enlarged that it resembles an oblong swollen fruit; but see discussion of geographic variation associated with hyperostosis of this pterygiophore in *C. hippos* species account. Even in small individuals of both species (where no pterygiophore swelling is evident), this bone is noticeably wider in lateral profile than in similar size individuals of *C. fischeri*, a species that never develops hyperostosis in this pterygiophore. The only site of hyperostosis in *C. senegallus* (largest specimen examined was 30 cm FL) is the posterior part of the supraoccipital crest. Hyperostosis is extensive in *C. bucculentus* Alleyne and Macleay and includes the entire supraoccipital crest, first supraneural, first pterygiophore of the dorsal and anal fins, and a pair of patches on the caudal fin near its base. The ribs on precaudal vertebrae 5–7 (*C. fischeri*) or 6–8 (*C. hippos*) exhibit extensive hyperostosis in relatively large individuals, but *C. fischeri* differs in that only the distal half of each rib is hyperossified. The only apparent contradiction to the consistent site

specificity of hyperostosis in the *C. hippos* group is the pattern of occurrence seen on ribs of *C. caninus*. Ribs of the fifth precaudal vertebra appear “normal” in nine specimens (359–643 mm FL), are strongly and uniquely hyperostotic in six others (335–431 mm FL), and in SIO 65–176A (670 mm FL) there is a slight but noticeable swelling only in the middle part of the rib. Even more unexpectedly, in two of six individuals only one rib of these bilaterally paired structures was strongly hyperostotic and its counterpart rib exhibited no hyperostosis.

*Caranx carangopsis* Steindachner, described from mid-Miocene deposits near Vienna, Austria, also deserves mention. Heckel (1852) recognized the distinctiveness of this fossil species and gave it a scientific name, but the subsequent description was prepared entirely by Steindachner (1859) who must be credited as author of the species. The original description is based on an incomplete series of disarticulated bones, some of which are clearly hyperostotic, from several individuals estimated to have been about 0.9 meters in length. The scientific name refers to the presumed close relationship of this fossil species to *C. carangus* (= *C. hippos*)—a relationship based, in part, on the occurrence of hyperostotic bones (including the ribs, some of the vertebrae, and the first dorsal-fin pterygiophore) in both species. The text descriptions and illustrations of the massively swollen first pterygiophore and pleural ribs of *C. carangopsis* agree reasonably well with those of western Atlantic *C. hippos*, but do not resemble that characteristic of eastern Atlantic *C. hippos*. Steindachner's (1859) accurate description (footnote on p. 690) of the swollen neural spines of the vertebrae in a 1220 mm TL *C. carangus* (= *C. hippos*) also contrasts sharply with his illustrations (pl. 7, Figs. 1–3) of the very differ-



ent thickened vertebrae of *C. carangopsis*. These fossil vertebrae are similar to those of hyperostotic *Trachurus trachurus* Linnaeus (see Desse et al., 1981), suggesting that the original description of *C. carangopsis* is likely based on material (deposited at NMW) from two carangid genera.

### Biology, fisheries, fish size, and edibility

Remarkably little information has been published on the biology of members of the *Caranx hippos* complex. Both Kwei (1978) and McBride and McKown (2000) discussed the importance of estuaries as nurseries for juvenile *C. hippos*, and such importance undoubtedly also applies to the other species. The former work is a comprehensive reference on the biology and fisheries of the "crevalle jack" in West Africa; unfortunately no photographs or meristic data were included that can be used to confirm the identification of species. *Caranx hippos* may well have been the most abundant species in the study, but *C. fischeri* is also very common in the region and almost certainly was included in some of the samples.

Noting the occurrence of smallest juveniles in his study, Berry (1959) stated that off the southeastern Atlantic coast of North America spawning probably occurred offshore from March to September. Kwei (1978) reported juveniles present in Ghanaian lagoons (Keta region) during every month of the year and re-entering the sea at sizes  $\geq 12$  cm FL. Large shoals of *Caranx* entered Ghanaian inshore waters from September to December, spawning appeared to be protracted, and peak spawning activity (determined from limited data) occurred from October to late January. Low frequency of ripe fish from inshore waters indicated that spawning occurred offshore. Thompson and Munro (1983) reported collecting seven "ripe" *C. hippos*, four males and three females, in the vicinity of Jamaica. The smallest ripe males and females were 55 and 66 cm FL, respectively. Adults were found occasionally in reef habitats and reproductively active fish were taken in May, July, and November. Hildebrand (1939) recorded seven females (67–98 cm TL) with large or developing roe and 11 males (69–88 cm TL), most with developed testes, during 20–24 February 1935 from Gatun Locks, Panama Canal. McBride and KcKown (2000) reported young-of-the-year *C. hippos*, <4.0 cm FL, present in subtropical estuaries (North Carolina to Florida) from June to November and discussed literature indicating that 9°C was likely the lower lethal temperature for the species. Franke and Acero (1993) suggested that *C. caninus* spawns throughout the year, peaking in January–February and August. Examining 96 specimens, they reported a 1:1 sex ratio, and the smallest mature males and females were 67 and 65 cm TL, respectively.

All species of the crevalle jack complex are major predators of small schooling fishes in coastal areas. In the western Atlantic (Florida, Louisiana, and Texas), Saloman and Naughton (1984) reported that small jacks fed primarily on clupeids and larger fish fed usually on clupeids, carangids, and sparids, but penaeoid

shrimps, crabs, and other invertebrates were also consumed. Clupeids (*Sardinella* and *Engraulis*) were also the dominant prey of *C. hippos* in the Gulf of Guinea, and juvenile shrimps contributed 50–80% of the diet of juvenile fish during the dry season (Kwei, 1978).

Most commercial landings of crevalle jack in the western Atlantic are from Florida, and annual catches of 221 to 320 t (metric tons) were recorded during 2000–2004 (NMFS<sup>2</sup>). In the eastern Atlantic, where data for *C. hippos* and *C. fischeri* are combined under "crevalle jack," commercial landings are reported only from Angola, Ghana, São Tome, and Principe, and for years 1995–2004 ranged from 2233 to 10,054 t (FAO, 2006). In the Gulf of Guinea, beach seine and set net fisheries for crevalle jack historically supported a large dried or salted fish industry. Okera (1978) reported *C. hippos* (as *C. carangus*) to be one of the dominate pelagic species in the beach seine fishery at Lumley, Sierra Leone, and that 80–100 cm TL fish were most common during September–October. Catches from Ghana in the mid 1950s to early 1960s and from Angola in the 1970s exceeded 15,000 t during some years, but such large catches no longer occur (FAO statistical data in Froese and Pauly<sup>3</sup>).

With regard to fighting ability of the crevalle jack, Shipp (1986) stated "there is no tougher game to be had in shallow coastal waters with light tackle than this species." *Caranx hippos* is more important in recreational fisheries in the United States (statistics based only on Atlantic Coast, Gulf of Mexico, excluding Texas and Puerto Rico) and for years 2000–2004 annual catches ranged from 409 to 1030 t (NMFS<sup>2</sup>). Recreational fishing also occurs in West Africa for both *C. hippos* and *C. fischeri* (Schratwieser<sup>4</sup>).

The IGFA All-Tackle world-record *C. hippos*, from Barra do Kwanza, Angola, was caught in December 2000, weighed 26.5 kg (58 lb 6 oz) and was 114 cm FL and 129 cm TL; several other fish almost as large have also been recorded from West Africa. One *C. fischeri* caught at Ozouri Zimbani, Gabon, in January 1989, weighed 20.9 kg, and was approximately 100 cm FL and 127 cm TL. An even larger one (see Fig. 8C), released without being measured or weighed (est. weight 26 kg) was caught in Loango National Park (Iguela Lagoon mouth), Gabon, in December 2005. The IGFA All-Tackle world-record *C. caninus* was caught at Playa Zancudo, Costa Rica, in March 1997, weighed 19.7 kg, and was 101.6 cm TL.

Crevalle jacks are strong fast-swimming predators with large quantities of red muscle and consequently

<sup>2</sup> NMFS (National Marine Fisheries Service). 2006. Fisheries Statistics Division. Website: <http://www.st.nmfs.gov/st1/> (accessed August 2006).

<sup>3</sup> Froese, R., and D. Pauly, eds. FishBase world wide web electronic publication. Website: <http://www.fishbase.org> version (07/2006) (accessed August 2006).

<sup>4</sup> Schratwieser, J. 2006. Personal commun. International Game Fish Association, 300 Gulf Stream Way, Dania Beach, Florida, 33004.



their flesh is generally considered coarse and relatively unpalatable. Small individuals are more flavorful and bleeding immediately after capture is recommended. According to Shipp (1986), some of the better seafood cooks make delectable marinated specialties using *C. hippos*.

***Caranx fischeri*, new species**

**Longfin crevalle jack**

(Figs. 1A, 4–7, 8, A–C, 11; Tables 1–4)

*Caranx hippos* (not of Linnaeus): Clark, 1915:385 (listed; Ascension Island); Fowler, 1919:254 (brief description; not distinct from American examples); Norman and Irvine, 1947:140, Fig. 65 (biology; artisanal fishery; Ghana); Tortonese, 1952:302, Figs. 11–12 (description; Mediterranean specimens and records); Franca, 1954:24, pl. 3 Figs. 2–3 (description; Luanda, Angola); Poll, 1954:131, Fig. 37, pl. 4, Figs. 1 and 3 (description); Cadenat, 1960:1392 (compared with "*C. carangus*"=*C. hippos*); Cadenat, 1961:240 (listed); Bauchot and Blanc, 1963:43, Fig. 2c (in part, composite description, also includes *C. hippos*; distribution); Daget and Stauch, 1968:40 (listed; Congo); Williams, 1968:252 (maximum reported size 75 cm); Blache et al., 1970:313, Fig. 818 (identification key; distinguished from "*C. carangus*"=*C. hippos*); Daget and Ittis, 1965:238, Fig. 152 (description; Ivory Coast); Tortonese, 1975:156, Fig. 64 (description; Mediterranean records, after Tortonese, 1952); Okera, 1978:85 (beach seine fishery, occasionally taken with "*C. carangus*"=*C. hippos*; Sierra Leone); Smith-Vaniz and Berry, 1981: unpaginated; Fig. (in part, composite description; distribution); Bianchi, 1986:49, Fig., color pl. II, Fig. 10 (habitat; biology; fisheries utilization; Angola); Smith-Vaniz, 1986:824, Fig. (in part, composite diagnosis; habitat; distribution); Bellemans et al., 1988:46, Fig., color pl. 2, Fig. 10 (local names; habitat); Papaconstantinou, 1988:95 (compiled; Greek seas); Edwards and Glass, 1987:1377 (unconfirmed records, St. Helena); Edwards, 1990:97, Fig. 48 (compiled description; unconfirmed occurrence at St. Helena); Smith-Vaniz et al., 1990:732 (in part, composite synonymy; distribution); Afonso et al., 1999:73 (listed; Gulf of Guinea); Bilecenoglu et al., 2002:84 (Aegean and Turkish seas; compiled); Edwards et al., 2003:2238 (J. R. Irvine's Ghanaian specimens).

*Caranx carangus* (non Bloch): Ehrenbaum, 1915:65 (misidentification, in part, Fig. of *C. hippos* after Goode, 1984; description; Cameroon); Chabanaud and Monod, 1927:18, Fig. 24 (listed, rare; Port Etienne, Mauritania); Collignon et al., 1957:192, Fig. 47 (brief description).

**Holotype** ANSP 140256 (328 mm FL), Cameroon, Douala, 22 Aug 1978, obtained by P. J. P. Whitehead.

**Paratypes** One-hundred twenty-eight specimens (33–530 mm FL) from 56 collections. SENEGAL:

IRSNB 829 (530), Dakar, Madeleine Island, 9 Nov 1949, G. Marlier; MNHN 1978-260 (313), coast of Senegal. GUINEA: ISH 163/62 (227), 9°45'N, 13°55'W, 17 m. SIERRA LEON: ANSP 158497 (237), Freetown, 8°29'24"N, 13°11'30"W, 6 m, hook and line, 9 Feb 1968, RV *Undaunted* Cr. 6801, G. Beardsley; ANSP 158498 (239), 7°07'N, 11°57'30"W, 18–21 m, Guinea Trawling Survey I, RV *La Rafale*, Trans. 12, sta. 1, 13 Nov 1963; BMNH 1928.8.3.14 (164.5), "Sierra Leone," J. Hornell; USNM 279566 (2, 163–203), St. Anne Banana Islands, 15–25 m, Feb 1986, G. Naylor. LIBERIA: USNM 193784 (121), Mesurado River beach, 6°19'N, 10°48'W, 24 May 1952, G. C. Miller; USNM 193790 (148) and USNM 193792 (102), Mesurado River beach, 20 Jun 1952, G. C. Miller; USNM 193779 (2, 148–163), Monrovia, Freeport, 5 May 1953, G. C. Miller. IVORY COAST: MNHN 1978-200 (253). GHANA: BMNH 1930.8.26.49-50 (2, 91–139), Accra, Mar 1930, F. R. Irvine (Irvine 53); BMNH 1938.12.15.48 (114), Volta River, Amedica, May 1938, F. R. Irvine (Irvine 237); BMNH 1939.7.12.12 (271), Prampram, Sep 1938, F. R. Irvine (Irvine 316); CAS-SU 64645 (118), Volta River; CAS-SU 64648 (124), Lower Volta River, Jun–Jul 1963, W. Titiat; CAS-SU 64700 (69), Battor River, 2 Mar 1964, T. R. Roberts; CAS-SU 66674 (41), Volta River at Amedia, 8 Mar 1963, T. R. Roberts; CAS-SU 69861 (2, 35–40), mouth of Volta River at Little Ada, 12 Jan 1963, T. R. Roberts; USNM 373240 (17, 33–52), Volta River at Big Ada, 9 Mar 1960, G. W. Bane; USNM 300660 (113), Tema Nunga, 18 May 1962, G. W. Bane; USNM 373242 (22, 37–52), beach at Tema fishing harbor, 15 Dec 1959, G. W. Bane; USNM 365702 (16, 71–90), Dix Cove Amaful, 25 Jan 1961, G. W. Bane; USNM 373244 (56), Ahiafo River W. of Amanful, Takoradi, 4 Feb 1961, Amegah; USNM 368973 (3, 49–88), Ashantee, Beyah River, 27 Nov 1889, W. H. Brown, U.S. Eclipse African Exped. TOGO: ZMH 14575 (155), lagoon near Anecto, "Dr. Liebl," summer 1909. BENIN: MNHN 1967-826 (198), 6°15'N, 2°38'E, 23 m, 27 Jul 1964, A. Crosnier and J. Marteau. NIGERIA: BMNH 1968.11.15.31-32 (2, 85–169), Lagos Lagoon, 1967, S. O. Fagade; ANSP 158495 (3, 154–163), 4°15'N, 6°49'E, 15 m, Guinea Trawling Survey II, RV *Thierry*, trans. 43, sta. 1, 5 Apr 1964; CAS 38373 (135), 6°21'N, 2°54'E, 15 m, Guinea Trawling Survey II, RV *Thierry*, trans. 36, sta. 1, 19 Mar 1964; CAS 38375 (2, 145–160), 4°28'N, 5°07'E, 19 m, Guinea Trawling Survey II, RV *Thierry*, trans. 41, sta. 7, 2 Apr 1964; CAS 38395 (2, 146–150), 5°15'N, 5°09'E, Guinea Trawling Survey II, RV *Thierry*, trans. 40, sta. 1, 30 Mar 1964; ISH 1147/64 (145), 5°09'N, 4°39'W, 20 m; ZMUC P.46362 (450), Bonny River, 22 Feb 1946, "Atlantidae" sta. 111; MNHN 1896-327 (153), Campagne Touree; BMNH 1956.9.6.68 (183), Lagos Tarkwe, F. Williams. CAMEROON: ANSP 140288 (156), Victoria, 23 Aug 1978, FAO; BMNH 1936.12. 29.7 (172), Victoria, Cross River; D. Tovey; CAS-SU 15883 (2, 41–44), Bwanjo, Bwanjo River, 15 Sep 1936, A. I. Good; CAS-SU 15884 (150), Kribi, 25 Oct 1938, A. I. Good; CAS-SU 15885 (171), Kribi, 23 Feb 1940, A. I. Good; CAS-SU 18221 (77), Mbode, 23 Dec 1940, A. I. Good; CAS-SU 18222 (82), Kribi, Kribi River, 24 Sep

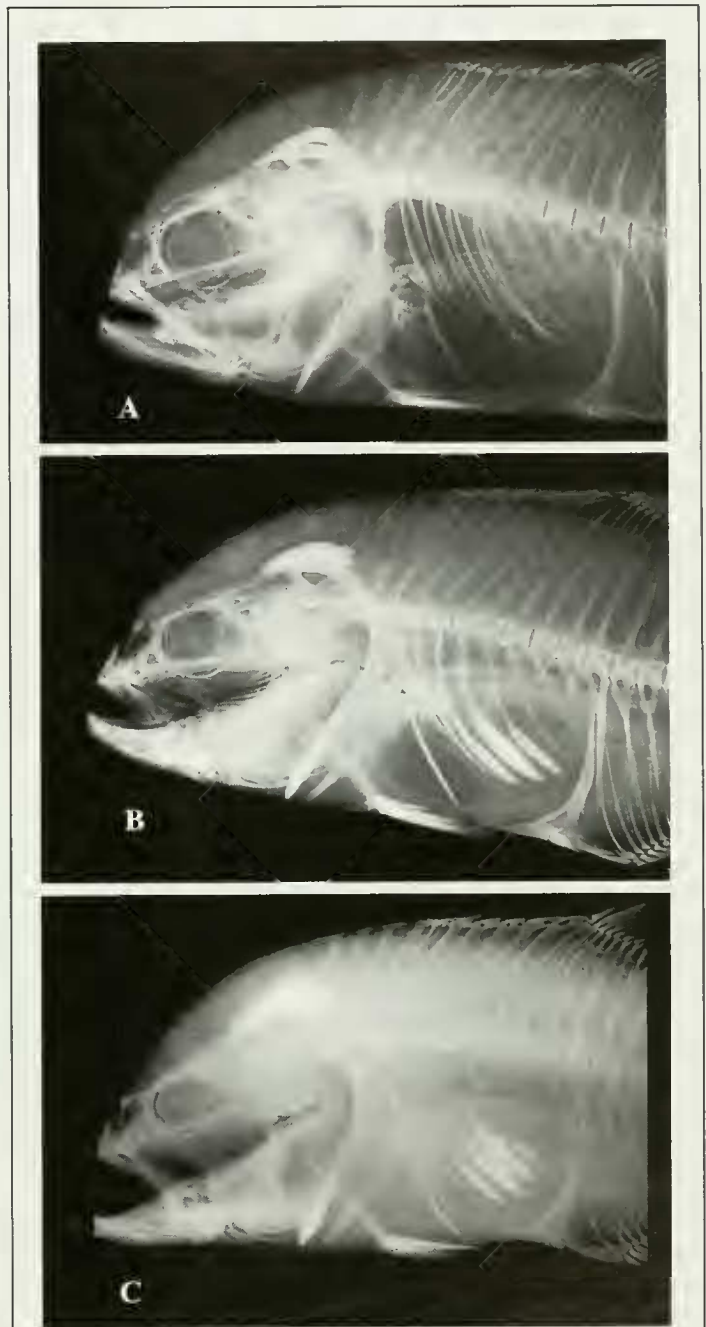
1940, A. I. Good; CAS-SU 64900 (70), Kirbi, Kirbi River, 23 Nov 1940, A. I. Good; MNHN 1978-336 (147), Depierre; MNHN 1982-1093 (117), Yabassi, Depierre, 1980. UF 142347 (2, 144–155), 2°28'N, 9°44'E, 15–16 m, Guinea Trawling Survey II, RV *Thierry* Trans. 49, sta. 1, 25 Apr 1968; USNM 304197 (81), S. Korup at coast, Rio del Rey, 10 Mar 1988, G. M. Reid; ZMH 14576 (135), Douala, J. V. Eitzen, 1912–1913. EQUATORIAL GUINEA: ANSP 158493 (4, 173–197), Bioko (Fernando Po) 3°35'N, 9°19'E, 30 m, Guinea Trawling Survey II, RV *Thierry*, trans. 47, sta. 2, 18 Apr 1964; UF 142348 (2, 52–64), Bioko (Fernando Po), fresh water pool on SE end of island, 25 Sep 1959, G. W. Bane. GABON: CAS 38376 (197), 0°21'N9°15'E, 20 m, Guinea Trawling Survey II, RV *Thierry*, trans. 52, sta. 1, 7 May 1964; BMNH 1896.5.5.14 (102), Corisco Island, M.H. Kingsley. CONGO: BMNH 1899.2.20.3 (173), Manyanga; BMNH 1899.11.27.87 (348), Banana; M. Delhez; MRAC 36 (403), Banana, 1896, Lt. E. Wilverth; MRAC 87428 (367), Banana, 1952, Major Marée. ASCENSION ISLAND: BMNH 1927.12.7.49 (358), J. Simpson.

**Other material** Centro Oceanográfico de Canarias, Tenerife, uncataloged (310), Benin, trawled in 38 m, 28 Jul 2002, FAO; SAIAB 26541 (130), Gulf of Guinea between Cameroon and Bioko; SAIAB 26541 (7, 138–233), Gulf of Guinea; MNHN 1978-235 (317), coast of tropical French Africa.

**Diagnosis** A member of the *Caranx hippos* complex with the following combination of characters: segmented dorsal-fin rays 21–23 (exceptionally 24); segmented anal-fin rays 17–19, usually 18; posttemporal bones hyperossified in specimens larger than 20 cm FL (Fig. 5); cleithrum, first pterygiophore of dorsal and anal fins, and neural spines of vertebrae relatively slender and never hyperossified; in specimens >20 cm FL, heights of longest dorsal- and anal-fin rays both 0.7–1.3 in head length; in adults, anal-fin lobe white anteriorly and remainder of fin gray to brown.

**Description** Total range of values given first, followed by values for holotype in parentheses: dorsal-fin rays VIII–I, 21–24 (22); anal-fin rays II–I, 17–19 (18); pectoral-fin rays 18–21 (21); vertebrae 10 pre-caudal + 14 caudal; curved lateral-line scales 50–73 (69); straight lateral-line scales 0–16 (4); straight lateral-line scutes 24–41 (35); total scales + scutes in straight lateral line 32–47 (39); developed gill rakers 2–7 (3) upper, 14–17 (14) lower, 16–24 (17) total; rudimentary gill rakers 0–4 (4) upper, 0–3 (3) lower, 4–8 (7) total; rudimentary + developed gill rakers 20–25 (24) total.

Posttemporal bones distinctly hyperossified in specimens larger than 20 cm FL (Fig. 5); cleithrum, pelvic bone, first pterygiophore of dorsal and anal fins, and vertebral neural spines not hyperossified, the latter

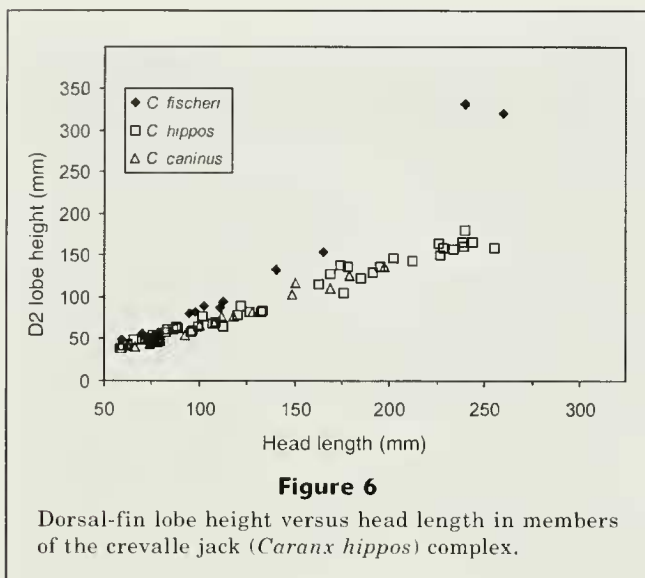


**Figure 5**

Radiographs of longfin crevalle jack (*Caranx fischeri*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (A) BMNH 1939.7.12.12, 271 mm FL, Gold Coast; (B) BMNH 1899.11.27.87, 348 mm FL, Congo; (C) ZMUZ P.46362, 450 mm FL, Nigeria.

relatively slender; in specimens  $\geq 34$  cm FL distal half of pleural ribs of vertebrae 5–7 hyperostotic; anterior dorsal-fin pterygiophore formula S/S-S/2+1/1; supraneurals relatively robust proximally; first anal-fin pterygiophore elongated anteroventrally.

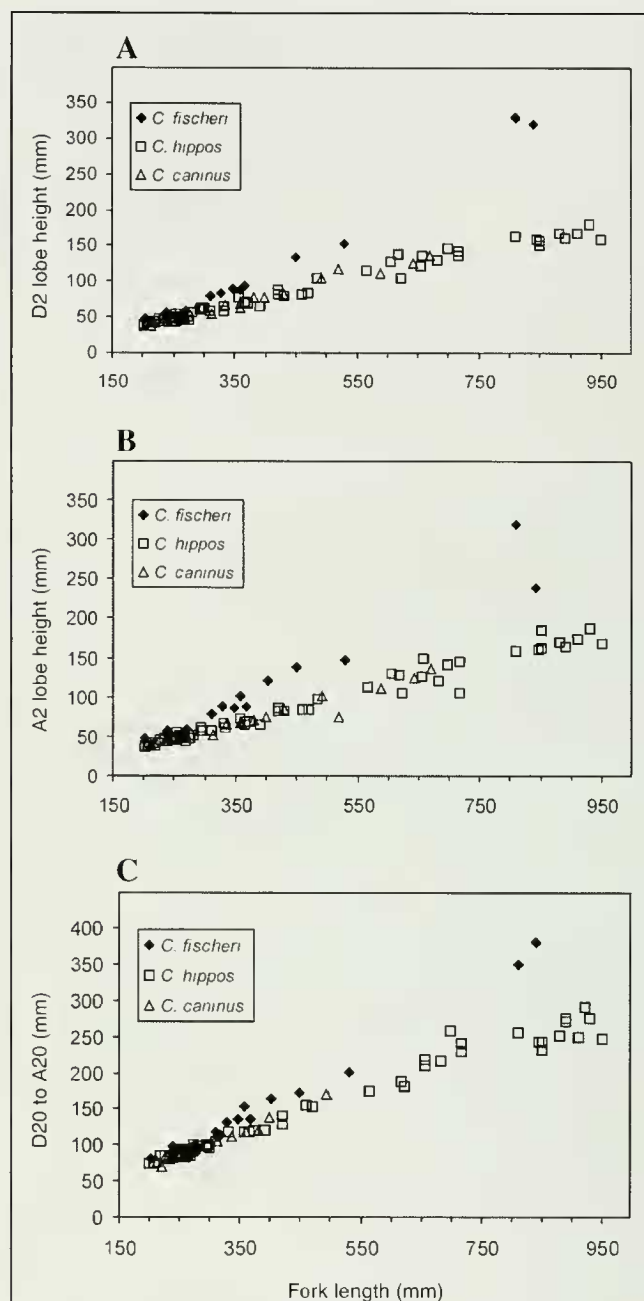




Body robust and compressed; head blunt—upper profile strongly convex, lower profile only slightly curved anteriorly; caudal peduncle slender. Breast naked ventrally to origin of pelvic fins, except for a small oval or oblong patch of scales in front of pelvic fins (Fig. 4); laterally, naked area sometimes extending slightly behind pelvic fins as a narrow wedge and always separated from naked base of pectoral fin by a narrow-to-broad band of scales; maxilla, lacrimal and dorsum of head naked; cheeks, preopercle, and opercle covered with scales; bases of dorsal and anal fins have a narrow scaly sheath anteriorly. Junction of curved and straight parts of lateral line below segmented dorsal-fin rays 5–10 (9); length of curved lateral line 0.93–1.47 (0.97) in straight lateral line. Dorsal fins well separated; first spine of spinous dorsal fin very slender and closely applied to second spine, posterior 1–4 spines partially or completely embedded in large adults; third spine longest and much shorter than height of second dorsal-fin lobe. Height of second dorsal-fin lobe 0.7–1.3 (1.2) in head length; height of anal-fin lobe 0.7–1.3 (1.1) in head length; heights of both fin lobes longer than head in large adults (Figs. 6–7). Pectoral fin of adults long and falcate, 0.8–0.9 (0.8) in head length.

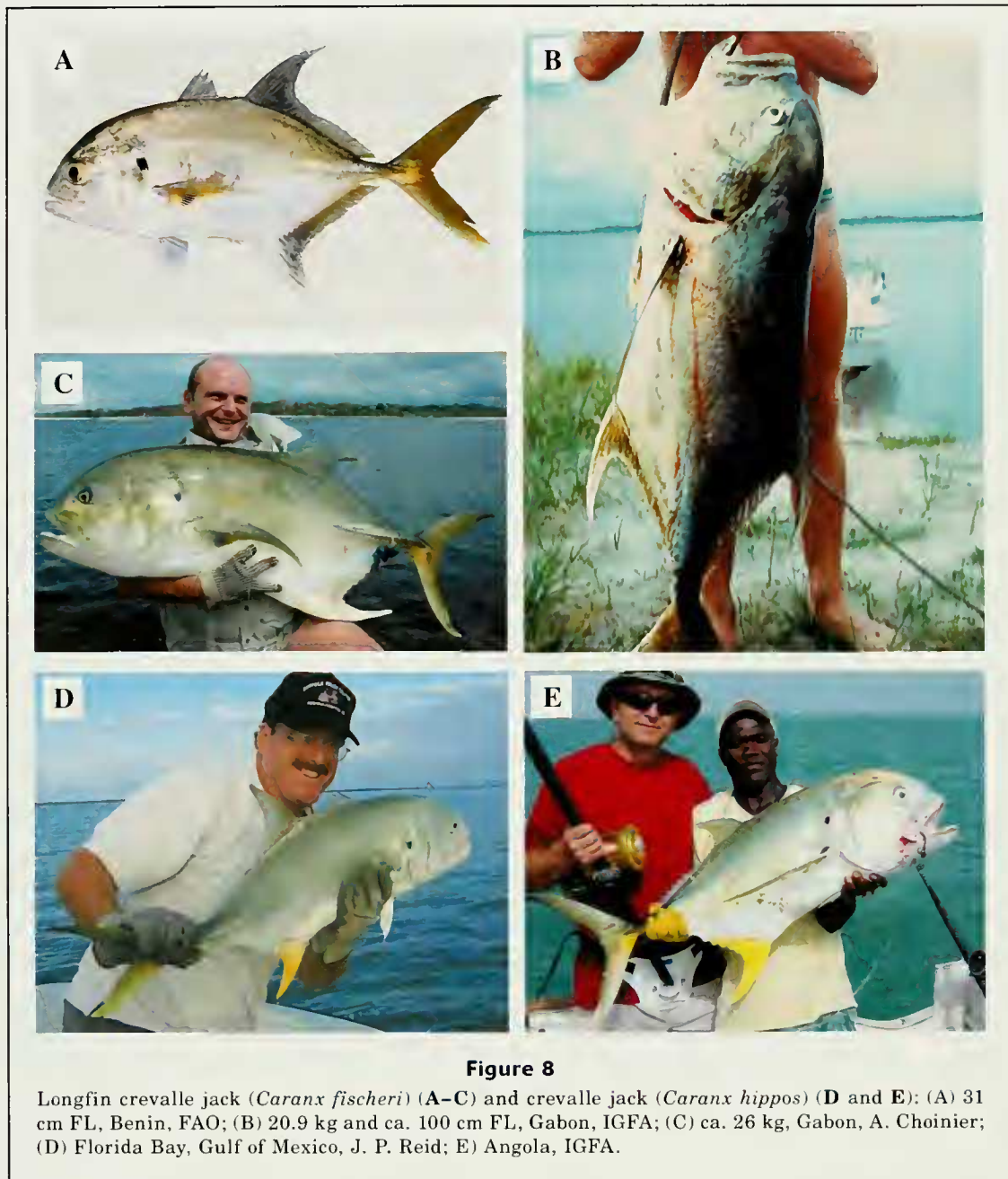
Upper jaw 2.2–2.3 (2.2) in head length, extending to or slightly behind posterior margin of eye; eye diameter 4.0–6.1 (4.3) in head length, and adipose eyelid well-developed, especially posteriorly, in adults. Upper jaw with an outer row of strong canines (widely spaced in adults) and an inner band of small villiform teeth that are widest anteriorly; lower jaw with a single row of strong conical teeth that are smaller anteriorly and one (occasionally two) pair of noticeably enlarged inner symphyseal canines. Vomerine tooth patch triangular-shaped, without a median posterior extension, and sparsely covered with small teeth.

Measurements of 14 paratypes, 203–530 mm, and the holotype as percentages of FL: snout to D1O 40.7–43.9



(41.6); snout to D2O 55.7–59.8 (57.0); snout to P2O 29.8–34.3 (30.2); snout to A2O 55.5–60.2 (58.8); D1O to P2O 33.4–39.0 (35.5); D2O to A2O 35.3–42.6 (40.2); D2 base 31.2–34.1 (32.2); A2 base 28.4–32.5 (28.7); curved lateral-line length 27.6–36.0 (34.3); straight lateral-line length 32.1–43.8 (33.3); height of dorsal-fin lobe 21.6–29.6 (25.3); height of anal-fin lobe 22.7–30.6 (26.8); pelvic-fin length 13.6–15.7 (13.9); pectoral-fin length 33.7–38.7





(36.4); head length 29.0–31.6 (29.9). As percentages of head length: postorbital head length 49.5–57.4 (50.5); snout length 24.4–28.4 (26.1); eye diameter 16.4–25.2 (23.1); upper jaw length 43.1–46.3 (45.2).

Fresh coloration of adults (Fig. 8, A–C) olive to greenish-blue dorsally, changing to silvery white on lower sides and ventrally; prominent black spot, approximately diameter of pupil, posteriorly on opercle at level of eye; an oval black spot on lower pectoral-fin rays and in upper axil of pectoral fins; dorsal fin dark brown; anal-fin lobe mostly white, especially anteriorly, and remainder of fin brownish-yellow; pelvic fins white and caudal fin brownish-yellow.

In preserved adults, the dark spot on the opercle and dark blotch on lower pectoral-fin rays are readily apparent, the latter on rays 6 or 7 to 14–16 (counting ventrally). The relatively pale anterior of the anal-fin lobe in comparison to the remainder of the fin is also evident. Small juveniles have five dusky bands on body; lack the dark blotch on the pectoral fin, have a heavily pigmented spinous dorsal fin and the dorsal-fin lobe is dark distally. Two juveniles, 35–40 mm FL (CAS-SU 69861) collected near the mouth of the Volta River, Ghana, had the identical pigmentation of 28 specimens of *C. hippos* (CAS-SU 64646) taken in the same collection, including some in the same size range. Berry

**Table 2**  
Frequency distributions of segmented dorsal- and anal-fin rays in the *Caranx hippos* species complex.

| Species                        | Dorsal-fin rays |     |    |    |    |    |          |           | Anal-fin rays |    |     |    |          |           |
|--------------------------------|-----------------|-----|----|----|----|----|----------|-----------|---------------|----|-----|----|----------|-----------|
|                                | 19              | 20  | 21 | 22 | 23 | 24 | <i>n</i> | $\bar{x}$ | 16            | 17 | 18  | 19 | <i>n</i> | $\bar{x}$ |
| <i>C. fischeri</i>             |                 |     | 31 | 93 | 10 | 1  | 135      | 21.9      |               | 17 | 104 | 14 | 135      | 18.0      |
| <i>C. hippos</i> (E. Atlantic) | 28              | 35  |    |    |    |    | 63       | 19.6      | 54            | 9  |     |    | 63       | 16.1      |
| <i>C. hippos</i> (W. Atlantic) | 18              | 130 | 13 |    |    |    | 161      | 20.0      | 103           | 58 |     |    | 161      | 16.4      |
| <i>C. caninus</i>              | 28              | 66  | 6  |    |    |    | 100      | 19.8      | 69            | 31 |     |    | 100      | 16.3      |

| Species                        | Dorsal + anal rays |    |    |    |    |    |    |    |    |          | Pectoral-fin rays |    |    |    |    |
|--------------------------------|--------------------|----|----|----|----|----|----|----|----|----------|-------------------|----|----|----|----|
|                                | 35                 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | <i>n</i> | $\bar{x}$         | 18 | 19 | 20 | 21 |
| <i>C. fischeri</i>             |                    |    |    | 15 | 18 | 83 | 13 | 5  | 1  | 135      | 39.8              | 1  | 12 | 57 | 12 |
| <i>C. hippos</i> (E. Atlantic) | 26                 | 30 | 7  |    |    |    |    |    |    | 63       | 35.7              | 1  | 18 | 21 | 1  |
| <i>C. hippos</i> (W. Atlantic) | 22                 | 79 | 51 | 9  |    |    |    |    |    | 161      | 36.3              | 3  | 68 | 50 | 2  |
| <i>C. caninus</i>              | 25                 | 47 | 22 | 6  |    |    |    |    |    | 100      | 36.1              |    | 15 | 38 | 8  |

(1959) included excellent illustrations of young *C. hippos* and *C. latus*. As both he and Laroche et al. (2006) discussed, small juveniles of these two species can not be distinguished solely by pigmentation. Thus, as might be expected, juveniles of *C. fischeri* and *hippos* also apparently cannot be distinguished by color pattern.

**Comparisons and relationships** The unique pigmentation of the pectoral fin in adults, pattern of breast squamation (a relatively small number of *C. hippos* and *C. caninus* are atypical in having the naked area of the breast continue without interruption to the pectoral-fin base), and the relatively large symphyseal dentary canines, which are shared by all members of the *hippos* complex, indicate their common ancestry. Of the three extant species, *C. fischeri* is readily distinguished by typically having more dorsal- and anal-fin rays (Table 2), and in specimens >20 cm FL the anterior dorsal- and anal-fin rays are relatively longer, and the body is deeper. The pattern of bones that exhibit hyperostosis is markedly different from that of the other species (Table 1), in neither of which is the posttemporal bone hyperossified. The anal-fin lobe is white anteriorly in adults of *C. fischeri*, in contrast to the uniformly lemon yellow lobe of *C. hippos*. Adults of *C. hippos* also differ in having the underside of the caudal peduncle bright yellow.

The presence of hyperostosis in a particular bone is presumed to be a derived condition (and conversely, the absence of hyperostosis is uninformative). On the basis of shared character states 5–6 (Table 1), *C. hippos* and *C. caninus* are considered to be sister species, and the geologically recent (~3.1 mya) rise of the Panamanian Isthmus was the likely vicariant event leading to the isolation and subsequent speciation of *C. caninus*. The common ancestor of *C. fischeri* and *C. hippos-caninus* presumably originated in the proto-Atlantic Ocean; and the sympatric occurrence of both *C. fischeri* and *C.*

*hippos* in the eastern Atlantic is likely indicative of an earlier phylogenetic origin.

**Distribution** African coast from Mauritania south at least to Moçamedes, southern Angola (Franca, 1954), and at least historically it was present in the Mediterranean Sea (Fig. 2). The collection of an adult *C. fischeri* from Ascension Island indicates at least the occasional vagrant occurrence at insular localities. Unconfirmed historical reports of *C. hippos* from both Ascension (Clark, 1915) and St. Helena (Edwards, 1990) are likely based on misidentifications, possibly of *C. fischeri*.

Tortonese (1952) discussed historical Mediterranean specimens dating from the 1890s in the Giglioli Collection and Genova Museum and he identified these specimens as *Caranx hippos*. Our efforts to locate these or recent Mediterranean specimens of *C. hippos* have been unsuccessful (see Tortonese, 1973, for status of historical fish collections in Italy). Data that Tortonese (1952) provided for two of his five specimens, as well as an accompanying photograph of one of them, confirm their identification as *C. fischeri*. We assume that all five specimens were conspecific, and all Tortonese's Mediterranean distributional records are plotted in Figure 2. Papaconstantinou (1988) and Bilecenoglu et al. (2002) cited a few additional unconfirmed literature records of *C. hippos* from the Mediterranean, which we presume were also based on misidentifications of *C. fischeri*; these records are not shown on the distribution map (Fig. 2). See discussion of probable erroneous recent photographic record of *C. hippos* from the Mediterranean in the following species account.

This species is often found in brackish water, sometimes ascending rivers. The paratype series includes collections, mostly of juveniles, from three different river drainages. In their account of *C. hippos*, Norman and Irvine (1947) quoted a secondary source as report-



ing that local fishermen say that *Afāfā* fish (probably *C. fischeri*) swim far up rivers to spawn.

**Etymology** We take great pleasure in naming this new species *Caranx fischeri* in honor of our friend and colleague Dr. Walter Fischer (retired) for his vision and dedication in initiating the Species Identification and Data Programme of the Food and Agriculture Organization of the United Nations (Fischer, 1989). In numerous ways this program has been an invaluable resource for marine fisheries biologists and ichthyologists generally.

***Caranx hippos* (Linnaeus, 1766)**

**Crevalle jack**

(Figs. 1B, 3, 6–7, 8, D–E, 9–13, 15; Tables 1–4)

*Scomber hippos* Linnaeus, 1766:494 (original description; Carolina; putative holotype Linn. Soc. Lond. 130 [Garden no. 16]); Wheeler, 1985:55 (type status).

*Scomber carangus* Bloch, 1793:69, pl. 340 (original description; Antilles; syntype ZMB 1542).

*Caranx erythrurus* Lacépède, 1801:58, 68 (no locality stated; based on *Caranx hippos* Linnaeus and other sources).

*Caranx carangua* Lacépède, 1801:59, 74 (original description; Martinique, West Indies; no type, based on a drawing by Plumier).

*Caranx antillarum* Bennett, 1840:282 (unnecessary replacement name for *Scomber carangus* Bloch 1793).

*Caranx defensor* DeKay, 1842:120, pl. 24, Fig. 72 (original description; New York; type whereabouts unknown).

*Carangus esculentus* Girard, 1858:168 (name only); Girard, 1859:23, pl. 11, Figs. 1–3 (description; Brazos Santiago, Texas; apparently an unnecessary replacement name for *Scomber carangus* Bloch to avoid “Strickland tautonymy” when Girard provided the new genus name *Carangus*).

*Caranx hippos*: Goode, 1884:323, pl. 99 (biology, edibility, distribution); Devincenzi, 1924:215, pl. 232, Fig. 1 (description; Rio de la Plata, Uruguay); Hildebrand, 1939:26 (sexual maturity; Panama Canal); Ginsburg, 1952:93, pl. 5, Fig. C (synonymy; description; distribution; Gulf of Mexico); Berry, 1959:503, Figs. 81–85 (juvenile description); Postel, 1959:157 (listed; Mauritania); Bauchot and Blanc, 1963:43 (composite description, also includes *C. fischeri*; distribution); Vergara, 1972 (osteology and relationships of Cuban *Caranx* spp.); Menezes and Figueiredo, 1980:4, Fig. 4 (brief description; Brazil); Smith-Vaniz and Berry, 1981:unpaginated (in part; composite description; distribution); Uyeno et al., 1983:332, color photo (description, Suriname); Shipp, 1986:118, Fig. 133 (habits; edibility; Gulf of Mexico); Scott and Scott, 1988:376 (Canadian occurrence); Smith-Vaniz et al., 1990:732 (composite synonymy; distribution); Cervigón, 1993:63, Figs. 24–25 (description; distribution; Venezuela); Randall, 1996:142, Fig. 173 (brief description; Caribbean); Murdy et al., 1997:165, Fig.

151 (description distribution; ecology; Chesapeake Bay); Debelius, 1997:159, unnumbered color Fig. (Balearic Islands, Spain; locality probably erroneous); Smith-Vaniz et al., 1999:238 (erroneous occurrence records; Bermuda); McBride and McKown, 2000:528 (seasonal dispersal patterns of juveniles between subtropical and temperate habitats; east coast of North America); Brito et al., 2002:220 (misidentification of *C. latus*; Canary Islands); Klein-MacPhee, 2002:415, Fig. 222 (description; early life history; Gulf of Maine); Laroche et al., 2006:1462, Figs. (early stages; early postflexion larvae indistinguishable from *C. latus*).

*Carangus hippos*: Jordan and Evermann, 1902:306, unnumbered photograph (color description; “everywhere a food-fish of considerable importance”).

*Caranx hippos tropicus* Nichols, 1920:45 (original description; Para, Brazil; holotype AMNH 3889).

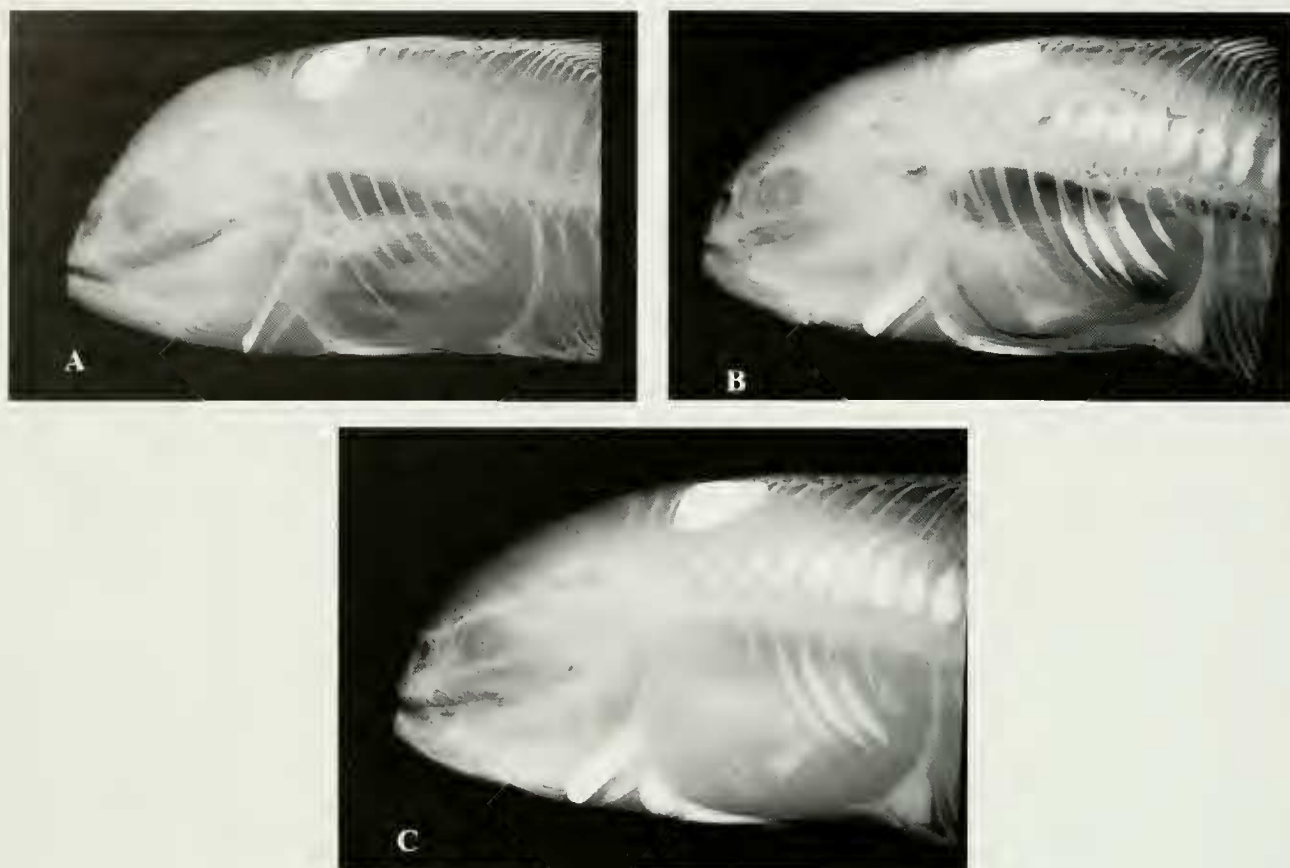
*Caranx africanus* (not of Steindachner): Poll, 1954: pl. 4, Fig. 4 (misidentification; Banana, Congo).

*Caranx carangus*: Cuvier and Valenciennes, 1833:91, pl. 57, Fig. 2 (description); Duméril, 1861:262 (listed; Gorée); Steindachner, 1870:704 (Senegal); Peters, 1877:836 (listed; Congo); Pellegrin, 1907:90, Fig. 7 (Dakar); Monod, 1927:699, Figs. 16–22B (Cameroun); Cadenat, 1950:171, Fig. 103 (Senegal); Cadenat, 1960:1392 (compared with “*C. hippos*” = *C. fischeri*; Ghana and Nigeria); Williams, 1968:252 (maximum reported size 120 cm); Blache et al., 1970:313, Fig. 819 (identification key; distinguished from “*C. hippos*” = *C. fischeri*); Okera, 1978:84 (abundance in beach seine fishery; Sierra Leone).

**Diagnosis** This species is a member of the *Caranx hippos* complex and has the following combination of characters: segmented dorsal-fin rays 19–21; segmented anal-fin rays 16 or 17; posttemporal bones never hyperossified; cleithra hyperossified distally in adults  $\geq 35$  cm FL (Figs. 9, 10); first pterygiophore of dorsal fin (Figs. 11, 12) and neural spines of some vertebrae (Fig. 13) noticeably (western Atlantic) or slightly to moderately (eastern Atlantic) hyperossified in adults  $\geq 50$  cm FL; first pterygiophore of anal fin not hyperossified in large adults; pleural ribs 6–8 hyperossified in large adults; in specimens  $> 20$  cm FL, heights of longest dorsal- and anal-fin rays 1.3–2.1 and 1.2–2.0, respectively, in head length; anal-fin lobe and underside of caudal peduncle bright yellow in adults.

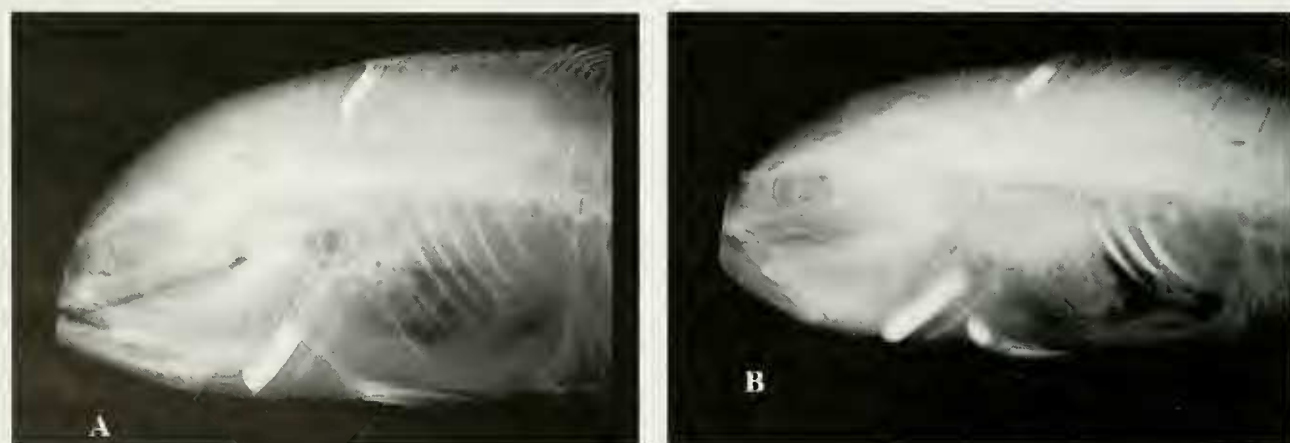
**Remarks** Nichols and Roemhild (1946) gave frequency counts of dorsal- and anal-fin rays for 42 specimens of *C. hippos* from the western Atlantic Ocean. Their counts of 15 anal soft rays (3 specimens) and 18 dorsal soft rays (2 specimens) were not duplicated (see Table 2) in our material that was based on a total of 161 western Atlantic and 63 eastern Atlantic specimens. Because Berry (1959, Table 21) recorded the same range of soft rays (based on 132 western Atlantic *C. hippos*) that we also recorded, we conclude that the outlier counts given in the earlier study are erroneous.





**Figure 9**

Radiographs of crevalle jack (*Caranx hippos*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (A) AMNH 58046, 274 mm FL, Brazil; (B) USNM 132964, 400 mm FL, Cuba; (C) USNM 114618, 557 mm FL, Guatemala.



**Figure 10**

Radiographs of crevalle jack (*Caranx hippos*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (A) MNHN 1978-216, 331 mm FL, Mauritania; (B) ZMUC 25, 565 mm FL, Senegal.

**Comparisons** Although long confused with *Caranx fischeri*, as discussed under "Comparisons and relationships" in the account of that species, *C. hippos* is easily distinguished. However, *C. hippos* and *C. caninus* are so similar externally that many authors considered them to be taxonomically identical or only subspecifically distinct. They have broadly overlapping mensural (Figs. 6–7) and meristic values (Tables 2–4), but the pattern of hyperostosis (Table 1) is surprisingly different in the two species. They differ in four character states (Table 1, characters 2–4, 6) and share three others (Table 1, characters 5–6), although even in one of these (Table 1, character 5), the relative degree of hyperostosis is different (Fig. 11), namely the expansion of the first dorsal-fin pterygiophore being more pronounced in *C. caninus*. The color of the anal fin of a living fish is lemon yellow in *C. hippos* and is either uniformly white or brownish-orange in *C. caninus*. The underside of the caudal peduncle in adults of *C. hippos* is mostly yellow, a trait that *C. Caninus* lacks.

**Distribution** This species is found on both sides of the Atlantic Ocean but is largely restricted to continental shelf areas (Fig. 2). In the western Atlantic it is found from Nova Scotia only as rare waifs (Scott and Scott, 1998) to Rio de la Plata, Uruguay (Devincenzi, 1924), but is absent from Bermuda (Smith-Vaniz et al., 1999) and most of the Lesser Antilles. Confirmed insular locality records based on museum specimens include those for Jamaica and the Bahamas (Andros Island), and we have photographic documentation for the Virgin Islands (St. Thomas) near the southern end of the shallow Puerto Rico shelf, where the species is relatively common. *Caranx hippos* is a regular summer visitor as far north as Woods Hole, Massachusetts (Klein-MacPhee, 2002), and young-of-the-year inhabit temperate estuaries of New York and New Jersey from July to November. McBride and McKown (2000) presented data indicating that these juveniles are spawned in subtropical latitudes and, aided by the Gulf Stream, disperse northward to coastal nurseries. Although the species is incapable of surviving the winter north of Cape Hatteras, growth rates and seasonal changes in distribution of this species indicate that some individuals successfully migrate southward to suitable over-wintering habitat and retain their potential contribution to the spawning population.

In the eastern Atlantic *C. hippos* is known from Mauritania to Angola, but historical records for the Mediterranean Sea (Tortonese, 1952, 1975) are based on misidentifications of *C. fischeri*, as presumably are additional unconfirmed records cited by Papaconstantinou (1988) and Bilecenoglu et al. (2002). The photograph (Debelius, 1997, p. 159) of a large school of adult *Caranx*, identified in the caption as *C. hippos* and stated to have been taken at the Balearic Islands, Spain, may have been a substitution and this locality record for the species could not be confirmed (Debelius<sup>5</sup>). Reports of *C. hippos* from the Canary Islands are based on misidentifications of *C. latus*; and

records of the species from the Azores (Arruda, 1997), Cape Verde Islands (Osório, 1911), and St. Helena (Melliss, 1875; Edwards and Glass, 1987; Edwards, 1990) are unreliable and can not be confirmed.

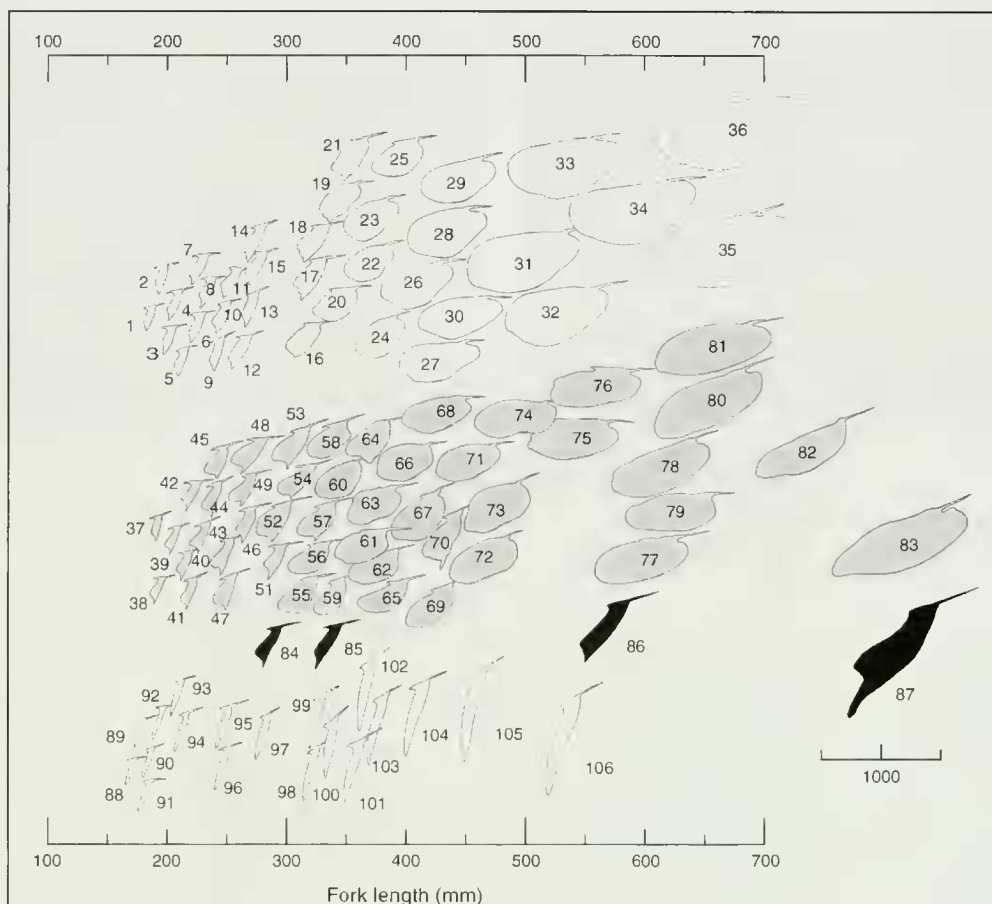
Adults are found inshore and frequently in upstream brackish waters (Klein-MacPhee, 2002) but are most common in salinities higher than 30 ppt (Gunter, 1945). Juveniles appear to use estuaries as nurseries in both temperate and tropical areas. Most reports of the species from freshwater are unreliable because of previous confusion with *C. fischeri* or are misleading (Herald and Strickland, 1949) because Homossassa Springs, Florida, has high alkalinity from the ionic composition of bicarbonate spring effluents. Gunter (1945) recorded juveniles and adults from Texas in salinities from 4.8 to 36.4 ppt. Smith (1985) reported that crevalle jacks are common summer residents in the Lower Hudson River, New York, and "in 1982 they were especially abundant as far upstream as River Mile 68 in early October and were still present at River Mile 66 in early November." McBride and McKown (2000) observed individuals in the Hudson River during July–October 1986–1993 at the freshwater interface (about 1 ppt), about 90–100 km inland.

**Geographic variation** Juveniles and adults of *C. hippos* from opposite sides of the Atlantic Ocean are virtually identical externally, including life coloration (Fig. 8, D–E), but differ notably in relative development of hyperostosis of the first pterygiophore of the dorsal fin. This bone is much less robust in adults of eastern Atlantic *C. hippos* (Figs. 11, 12). There is some variation in relative development of this pterygiophore in large western Atlantic specimens, but in all those we have examined (including a number of partially articulated skeletons at the AMNH not listed below) it is dorsolaterally expanded in marked contrast to the slender profile of the bone in eastern Atlantic specimens (Fig. 12). The basal halves of the neural spines of some of the anterior vertebrae (usually vertebrae 5–12) are also consistently and strongly expanded (Fig. 9, B–C) in large adults from the western Atlantic. The neural spines are only slightly hyperossified in a 56-cm-FL specimen (Figs. 10B, 13) from Senegal. They were more expanded (although much less so than in similar-size western Atlantic specimens) in a 90-cm specimen from Angola that had been partially dissected and photographed at our request so that we could ascertain the condition of the neural spines.

*Caranx hippos* has an essentially continental distribution (there are no confirmed records from any oceanic island) and populations on opposite sides of the Atlantic presumably are isolated and have little genetic connectivity, thus some geographic differentiation might be expected. *Caranx senegallus* and *C. fischeri* are both eastern Atlantic endemics, but other Atlantic species of *Caranx* with amphi-Atlantic distributions (*C.*

<sup>5</sup> Debelius, H. 2004. Personal commun. IKAN-Unterwasserarchiv, Waldschulstrasse 166, 65933, Frankfurt, Germany.





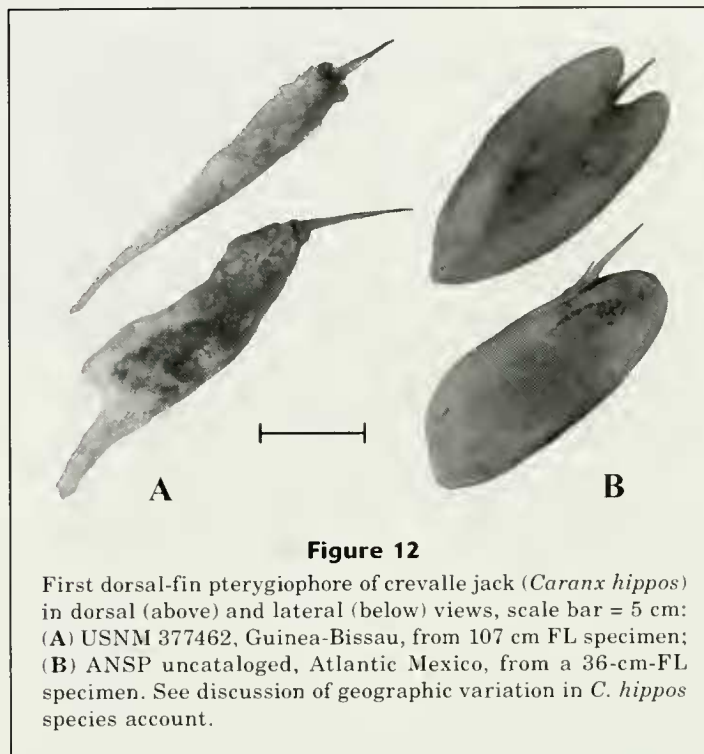
**Figure 11**

First dorsal-fin pterygiophore in lateral view (anterior of pterygiophore on left). Outlines were traced from radiographs plotted against fork length of Pacific crevalle jack (*Caranx caninus*) (pterygiophores numbers 1–36), crevalle jack (*C. hippos*) (37–83, western Atlantic, 84–87 eastern Atlantic, in black), and longfin crevalle jack (*C. fischeri*) (88–106). Numbers correspond to those given in Appendix 1 with associated catalog numbers, specimen sizes and localities.

*crysos*, *C. latus*, and *C. lugubris*) commonly are found at insular localities, including Ascension Island on the mid-Atlantic ridge.

**Material examined** Two hundred fifty-one specimens (29.5–1070 mm FL) from 103 collections (western Atlantic localities abbreviated). MASSACHUSETTS: ANSP 165909 (4, 152–189); USNM 10431 (4, 262–276); USNM 13656 (265); USNM 126812 (2, 54–69). RHODE ISLAND: ANSP 98280 (2, 175–179); USNM 21654 (274). NEW JERSEY: ANSP 97864 (3, 176–189); ANSP 121305 (2, 167–175); ANSP 105515 (173); ANSP 165911 (118); USNM 37022 (187); USNM 45120 (133); USNM 64053 (186). DELAWARE: USNM 187280 (5, 102–120), Indian River. VIRGINIA: ANSP 52647 (167). NORTH CAROLINA: UF 124148 (153) and UF 124400 (154), Onslow Bay. SOUTH CAROLINA: UF 124149 (122). GEORGIA: UF 126976 (2, 132–133). FLORIDA: CAS 216873 (1015); ANSP 33039 (188); ANSP 93821 (366);

ANSP 151093 (6, 186–208); CAS 216873 (1015); USNM 12681 (3, 254–269); USNM 22855 (622); USNM 29986 (372); USNM 53335 (263); USNM 57225 (260); USNM 57294 (2, 176–187); USNM 57295 (2, 172–175); USNM 154847 (167), St. Johns River; USNM 184871 (366); USNM 332457 (2, 390–421), Swanee River, salinity 14 ppt; USNM 362541 (3, 430–490), Caloosahatchee River; USNM 62289 (219); USNM 163601 (227). ALABAMA: ANSP 162288 (9, 810–950); USNM 157710 (4, 138–154). TEXAS: ANSP 99176 (5, 96–105); USNM 708 (10, 30–93); USNM 118497 (122); USNM 144017 (153). BAHAMAS: ANSP 102112 (2, 293–297); ANSP 102762 (657). CUBA: USNM 9867 (177); USNM 19821 (2, 357–386); USNM 132964 (2, 303–400). JAMAICA: USNM 32080 (725). DOMINICAN REPUBLIC: ANSP 81949 (114). PUERTO RICO: ANSP 151589 (254); ANSP 151590 (182). MEXICO: ANSP 159674 (5, 655–717); ANSP 156991 (9, 159–174); USNM 39278 (311); USNM 50473 (281). GUATEMALA: USNM 114580 (333); USNM



**Figure 12**

First dorsal-fin pterygiophore of crevalle jack (*Caranx hippos*) in dorsal (above) and lateral (below) views, scale bar = 5 cm: (A) USNM 377462, Guinea-Bissau, from 107 cm FL specimen; (B) ANSP uncataloged, Atlantic Mexico, from a 36-cm-FL specimen. See discussion of geographic variation in *C. hippos* species account.

114594 (420), 2 mi above mouth of Rio Sarstoon; USNM 114618 (7, 326–557); USNM 134378 (92); USNM 157572 (196). HONDURAS: ANSP 158504 (5, 227–251). COSTA RICA: USNM 89073 (122); USNM 94155 (114). PANAMA: ANSP 45238 (2, 119–136); USNM 79965 (287); USNM 79981 (440); USNM 128657 (2, 350–364); USNM 128658 (334). COLOMBIA: USNM 94769 (2, 142–158); USNM 290077 (247). CURACAO: USNM 34914 (263). VENEZUELA: ANSP 161642 (2, 202–209); USNM 121801 (9, 136–213). GUYANA: USNM 186190 (357). FRENCH GUIANA: ANSP 148238 (294). BRAZIL: AMNH 3889 (300), Para Mkt., holotype of *Caranx hippos tropicus*; AMNH 58046 (274); ANSP 121329 (102); CAS 11861 (178); CAS-SU 22133 (4, 223–235); CAS-SU 51828 (2, 216–235); CAS-SU 51830 (231); CAS-SU 53013 (300); CAS-SU 53015 (311); CAS-SU 53016 (3, 316–319); CAS-SU 53025 (233); CAS-SU 53026 (232); CAS-SU 53080 (2, 605–617); CAS-SU 53082 (2, 534–555). MAURITANIA: MNHN 1978-216 (331), Port Etienne. SENEGAL: BMNH 1900.6.28.302–303 (2, 95–109), St. Louise, M. P. Delhez; ZMUC 25 (565), Senegal, Dakar, Dec 1927, H. Madsen. GUINEA-BISSAU: USNM 377462 (estimated 107 cm) anterior dorsal-fin pterygiophore, May 2004, P. Sebile. LIBERIA: ANSP 158494 (16, 29.5–35.0), 6°31'–7°07'N, 11°29'–11°57'30"W, surface dip net, 12 Nov 1963, B. B. Collette, sta. BBC 888. GHANA: CAS-SU 64646 (28, 34.8–68.4), mouth of Volta River at Little Ada, 12 Jan 1963, T. R. Roberts; USNM 373239 (3, 33–52), Volta River at Big Ada, 9 Mar 1960, G. W. Bane; USNM 42228 (71), Ashantee, Beyah River, 27 Nov 1889, W. H. Brown; USNM 373241 (3, 48–57), beach at Tema fishing harbor, 15 Dec 1959, G. W. Bane;

USNM 373247 (66), 0.4 km above mouth of Rio Hwini, Takoradi, 26 Nov 1959, G. W. Bane; USNM 300496 (78), Takoradi swimming pool, 10 Aug 1961, G. W. Bane; USNM 368825 (65), Takoradi Fisheries Station bay, 14 Aug 1961, G. W. Bane. NIGERIA: MNHN 1896-328 (150), Campagne Toutee; BMNH 1968.11.15.29-30 (2, 93–94), Lagos Lagoon, 1967, S. O. Fagade. EQUATORIAL GUINEA: MNHN 1893-14 (155), Pobeguín. CONGO: MNHN 1967-0286 (88), Tchitemo, May 1964, A. Stauch. WEST AFRICA: MNHN 1978-230 (274) “coast of tropical French Africa.”

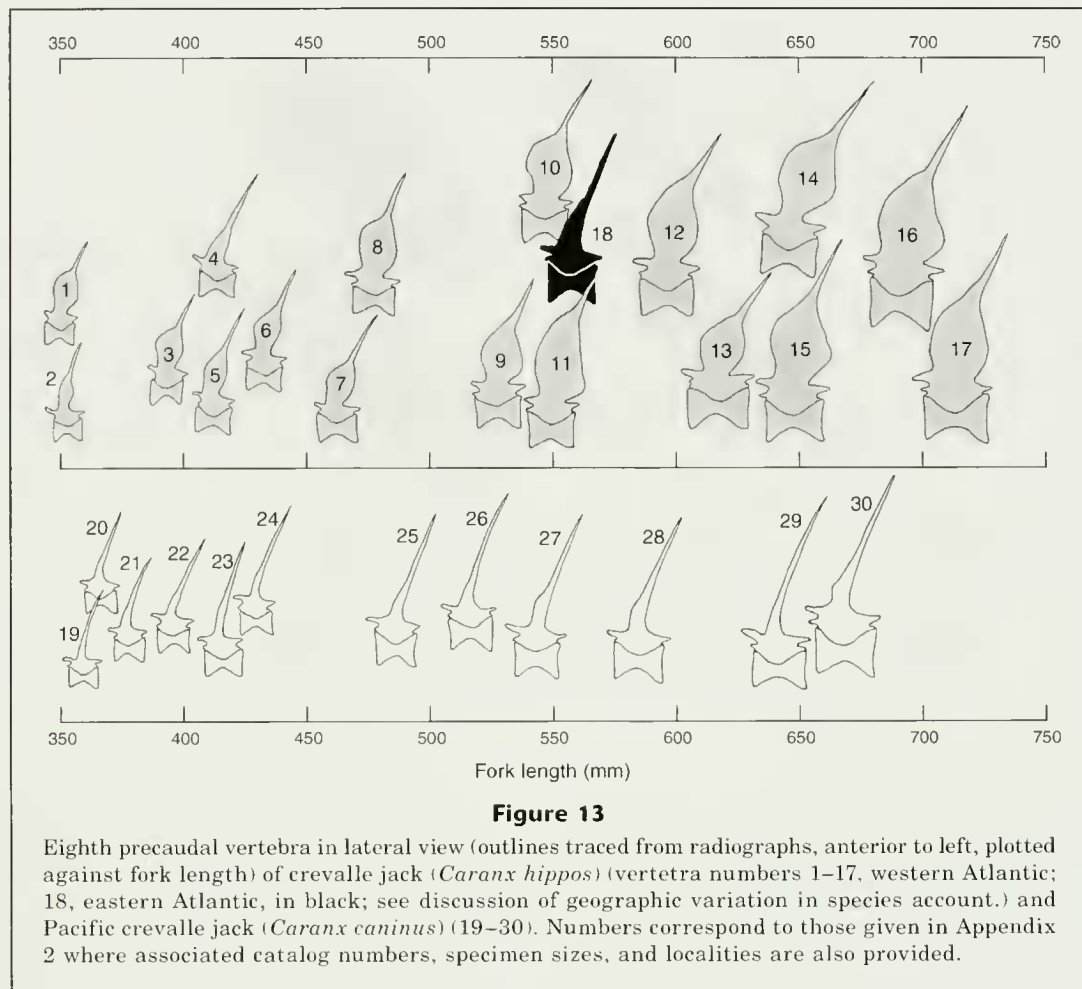
***Caranx caninus* Günther, 1867**

**Pacific crevalle jack**

(Figs. 1C, 6–7, 11, 13–15; Tables 1–4)

*Caranx caninus* Günther, 1867:601 (original description; Panama; holotype BMNH 1863.12.16.19); Günther, 1868:432 (expanded description); Walford, 1937:72, color pl. 51, Fig. A (diagnosis; comparison with *C. hippos*; habits); Walford, 1974:15 (“disagreement among ichthyologists as to whether species is distinct from *C. hippos*,” distribution); Eschmeyer and Herald, 1983, Fig. 40 (diagnosis; possible synonym of *C. hippos*; distribution); Allen and Robertson, 1994:126, pl. VIII-4 (color photograph; brief description); Franke and Acero, 1993:57 (size at sexual maturity; Colombia); Grove and Lavenberg, 1997:362, Figs. 37 (color), 192, 193 (brief description; Galapagos); Garrison, 2000:166, color photograph (uncommon; Costa Rica, Cocos Island); Lea and Rosenblatt, 2000:122 (occurrence in San Diego Bay).





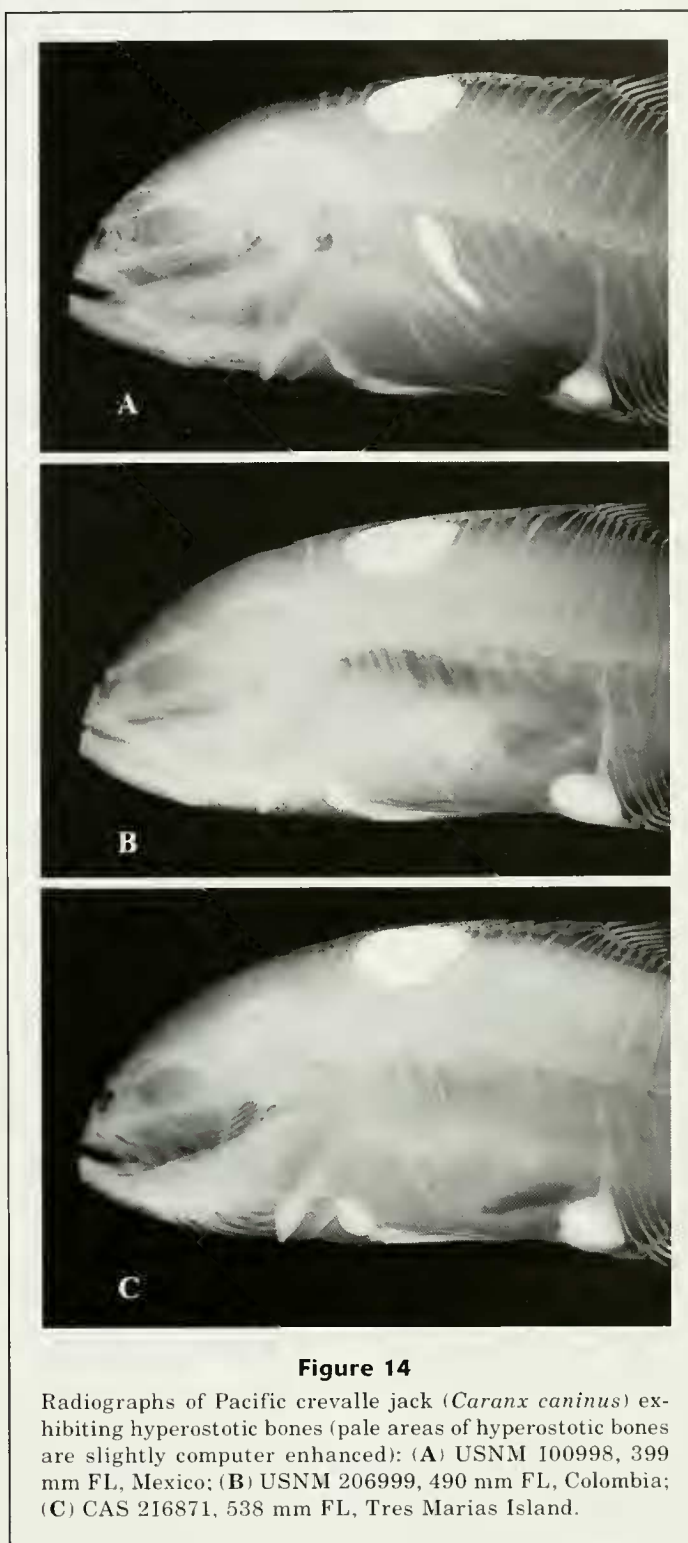
*Caranx hippos* (not of Linnaeus): Jordan and Gilbert, 1883:201 (synonymy; in part; *C. caninus* listed as synonym); Jordan, 1895:432 (misidentification in part; important food fish, occasionally entering estuaries; specimens from west coast and Havana indistinguishable; Mazatlan); Gilbert and Starks, 1904:77 (misidentification in part; Pacific and Atlantic specimens compared and considered conspecific; Panama Bay); Nichols, 1920:44 (Gulf of California fish indistinguishable from those from Atlantic coast); Meek and Hildebrand, 1925:350 (misidentification in part; distribution "Panama, common on both coasts of tropical America"); Hildebrand, 1946:208 (description; Peru); Fierstine, 1968:1, Figs.1–5 (description of dorsal-fin pterygiophore hyperostosis in Miocene deposits and living *Caranx*); Berry, 1974:240 (eastern Pacific and western Atlantic specimens essentially identical); Amezcua-Linares, 1996:88, unnumbered Fig. (description; biology; Mexico); Castro-Aquirre and Balart, 2002:166 (listed; Revillagigedo Islands).

*Caranx* (*Tricropterus*) *hippos*: Hiyama, 1937:33, color pl. 12 ("often identified to *C. caninus* Günther; reaches 2 feet, abundant, good food fish").

*Caranx hippos caninus*: Nichols, 1937:58 (specimens from Ecuador compared with Atlantic *C. hippos*); Hobson, 1968:63, fig. 25 (predatory behavior; Gulf of California).

**Diagnosis** A member of the *Caranx hippos* complex with the following combination of characters: segmented dorsal-fin rays 19–21 (Table 2); segmented anal-fin rays 16 or 17; posttemporal bones, cleithra, and neural spines of vertebrae never hyperossified (Fig. 14); first pterygiophore of dorsal fin distinctly hyperossified in adults  $\geq 38$  cm FL (Figs. 11, 14); first pterygiophore of anal fin distinctly hyperossified, and having a convex anterior profile, in adults  $>40$  cm FL (Figs. 14, B–C, 15); either none or 5th pleural rib only hyperossified (Fig. 14A) in adults  $\geq 38$  cm FL; in specimens  $>20$  cm FL, heights of longest dorsal- and anal-fin rays 1.3–1.7 and 1.3–2.0 mm, respectively, in head length; and anal-fin lobe varying from entirely white to brownish-orange in adults.

**Comparisons** *Caranx caninus* and *C. hippos* have identical or broadly overlapping mensural and meristic values (Tables 2–4), although *C. caninus* usu-

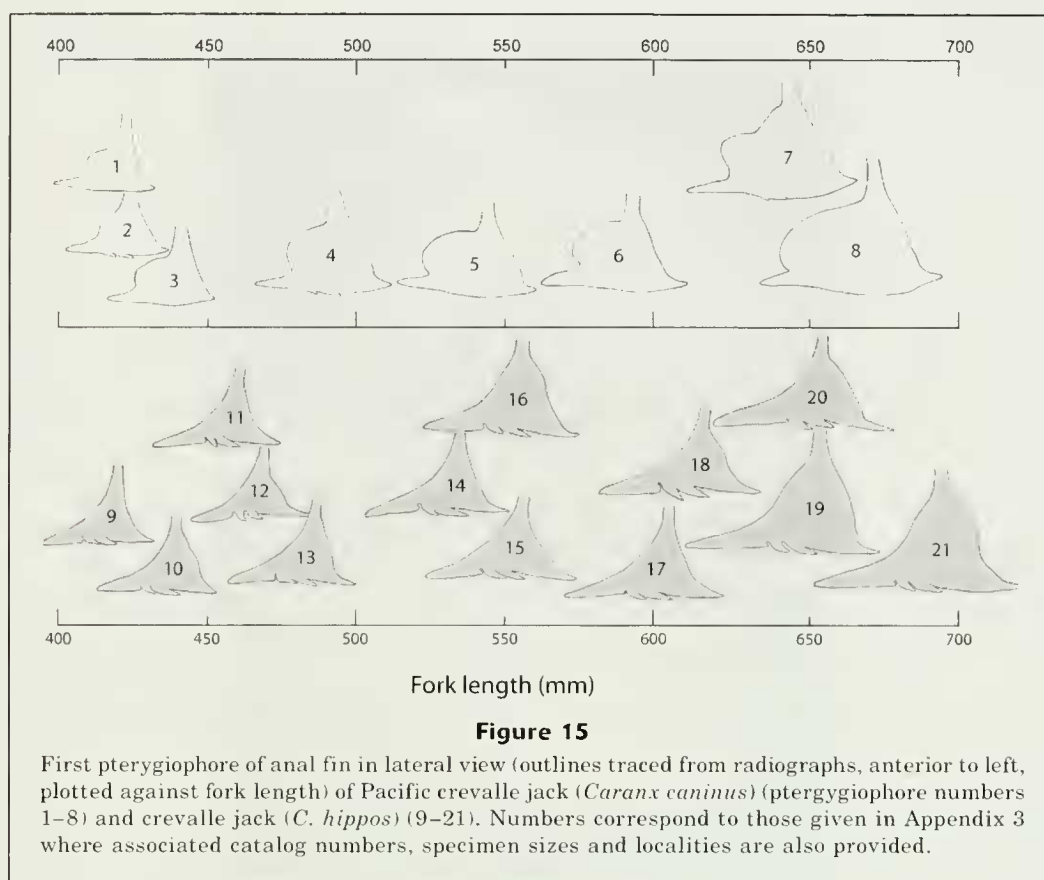


**Figure 14**

Radiographs of Pacific crevalle jack (*Caranx caninus*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (A) USNM 100998, 399 mm FL, Mexico; (B) USNM 206999, 490 mm FL, Colombia; (C) CAS 216871, 538 mm FL, Tres Marias Island.

ally has more lateral-line scutes. Differences in development of hyperostosis (Table 1) are the most useful distinguishing characters (see comparisons in account of *C. hippos*). The color of the anal fin also differs in these two species. In *C. hippos* the anal

fin is consistently lemon yellow, fading in postmortem individuals to orange-yellow. The anal fin of *C. caninus* varies from uniformly white to brownish-orange, and often some of the interradiation membranes are dark brown. According to photographs of angler-



caught fish, the underside of the caudal peduncle of *C. caninus* is never bright yellow as in *C. hippos*, and in fish with uniformly white anal fins the caudal peduncle is also white.

**Remarks** We have not had the opportunity to study *C. caninus* in the field although we have examined many color photographs of recently caught adults. The pronounced differences in color of the anal fin in this species (see above) indicate the possibility of sexual dichromatism but determining the sex of large *Caranx* is best done with freshly caught specimens. The striking and inconsistent occurrence of hyperostosis of the third rib in this species (see Table 1) is also puzzling and the possibility that its presence or absence in adults may be sex linked and should be investigated.

**Distribution** This species is restricted to the eastern tropical Pacific (Fig. 2), ranging north to San Diego Bay, California, where its occurrence is associated with El Niño events (Lea and Rosenblatt, 2000), and from Mexico south to Lobos de Tierra Island, Peru (6°27'S); also known from the Galapagos, Malpelo, Cocos, and Revillagigedo islands, but it is unrecorded from Clipperton Atoll (Robertson and Allen, 1996). Meek and Hildebrand (1925) reported the species, as *C. hippos*, from tidal streams at Corozal and Balboa, Panama.

**Material examined** One hundred ten specimens (59–670 mm FL) from 51 collections. CALIFORNIA: SIO 75-383 (643), San Diego Bay. TRES MARIAS IS.: CAS 216871 (538); MEXICO: ANSP 144417 (25, 98–176); ANSP 158506 (4, 248–313); CAS 66825 (155); CAS 11112 (329); CAS-SU 55737 (2, 180–182); CAS 216872 (421); SIO 62-61 (3, 372–420); SIO 62-2725 (377); SIO 65-176A (670); SIO 65-182 (431); USNM 28293 (304); USNM 29556 (152); USNM 29617 (156); USNM 47143 (185); USNM 47144 (213); USNM 47145 (191); USNM 100991 (381); USNM 100998 (399); USNM 101006 (261); USNM 205166 (307). GUATEMALA: USNM 114469 (8, 77–233); EL SALVADOR: ANSP 136539 (172); ANSP 144401 (220); ANSP 144406 (169); USNM 220728 (2, 240–248); USNM 367522 (185); USNM 367542 (156); USNM 367671 (81); USNM 367946 (8, 61–77); USNM 367968 (63); USNM 367990 (166). PANAMA: ANSP 144409 (163); CAS 42539 (333); CAS 66826 (177); CAS 89955 (201); USNM 82080 (7, 75–187); USNM 79984 (2, 335–348); USNM 128659 (520); USNM 226417 (4, 59–112); USNM 321987 (2, 67–84). COLOMBIA: ANSP 144413 (164); USNM 206999 (493). ECUADOR: ANSP 158998 (137); CAS 66938 (212). GALAPAGOS IS.: USNM 89751 (2, 109–121), Indefatigable Id. PERU: SIO 58–83 (588); USNM 127917 (158); USNM 127918 (359); USNM 127919 (360).



**Table 3**  
Frequency distributions of lateral-line scales and scutes in the *Caranx hippos* species complex.

| Species                        | Curved lateral-line scales            |    |    |    |    |    |    |    |    |    |    |           |           | n         | $\bar{x}$ | SD  |
|--------------------------------|---------------------------------------|----|----|----|----|----|----|----|----|----|----|-----------|-----------|-----------|-----------|-----|
|                                | 50                                    | 52 | 54 | 56 | 58 | 60 | 62 | 64 | 66 | 68 | 70 | 72        | 74        |           |           |     |
|                                | 51                                    | 53 | 55 | 57 | 59 | 61 | 63 | 65 | 67 | 69 | 71 | 73        | 75        |           |           |     |
| <i>C. fischeri</i>             | 1                                     | —  | 3  | 6  | 6  | 6  | 11 | 8  | 9  | 3  |    | 1         |           | 54        | 62.1      | 4.5 |
| <i>C. hippos</i> (E. Atlantic) |                                       |    |    |    |    | 1  | 1  | 3  | 1  | 5  | —  | 1         |           | 12        | 66.2      | 3.3 |
| <i>C. hippos</i> (W. Atlantic) |                                       |    | 1  | 1  | 3  | 7  | 7  | 12 | 14 | 13 | 10 | 4         | 1         | 73        | 66.0      | 4.1 |
| <i>C. caninus</i>              |                                       | 1  | 1  | —  | 5  | 3  | 9  | 10 | 8  | 4  | 2  | 1         |           | 44        | 61.8      | 4.1 |
| Species                        | Straight lateral-line scales          |    |    |    |    |    |    |    |    |    | n  | $\bar{x}$ | SD        |           |           |     |
|                                | 0                                     | 1  | 3  | 5  | 7  | 9  | 11 | 13 | 15 |    |    |           |           |           |           |     |
|                                | 0                                     | 2  | 4  | 6  | 8  | 10 | 12 | 14 | 16 |    |    |           |           |           |           |     |
| <i>C. fischeri</i>             | 5                                     | 6  | 21 | 12 | 19 | 6  | —  | —  | 1  |    |    |           |           | 70        | 5.5       | 2.8 |
| <i>C. hippos</i> (E. Atlantic) | 1                                     | 1  | 4  | 5  | 3  | 2  | —  | —  | 1  |    |    |           |           | 17        | 5.9       | 3.4 |
| <i>C. hippos</i> (W. Atlantic) | 4                                     | 10 | 21 | 19 | 13 | 8  | 5  | 1  | 1  |    |    |           |           | 82        | 5.4       | 3.2 |
| <i>C. caninus</i>              | 8                                     | 9  | 17 | 11 | 7  | 1  | 1  |    |    |    |    |           |           | 54        | 3.8       | 2.7 |
| Species                        | Straight lateral-line scutes          |    |    |    |    |    |    |    |    |    |    |           | n         | $\bar{x}$ | SD        |     |
|                                | 24                                    | 26 | 28 | 30 | 32 | 34 | 36 | 38 | 40 | 42 | 44 | 46        |           |           |           |     |
|                                | 25                                    | 27 | 29 | 31 | 33 | 35 | 37 | 39 | 41 | 43 | 45 | 47        |           |           |           |     |
| <i>C. fischeri</i>             | 3                                     | 3  | 15 | 8  | 19 | 17 | 2  | 2  | 1  |    |    |           |           | 70        | 31.8      | 3.3 |
| <i>C. hippos</i> (E. Atlantic) | 4                                     | 1  | —  | 6  | 3  | 1  | 2  |    |    |    |    |           |           | 17        | 29.9      | 4.2 |
| <i>C. hippos</i> (W. Atlantic) | 1                                     | 4  | 12 | 26 | 27 | 8  | 3  | 1  |    |    |    |           |           | 82        | 31.2      | 2.4 |
| <i>C. caninus</i>              |                                       |    | 1  | —  | —  | 8  | 15 | 16 | 7  | 5  | 1  | 1         |           | 54        | 38.1      | 2.9 |
| Species                        | Straight lateral-line scales + scutes |    |    |    |    |    |    |    |    |    |    | n         | $\bar{x}$ | SD        |           |     |
|                                | 28                                    | 30 | 32 | 34 | 36 | 38 | 40 | 42 | 44 | 46 | 48 |           |           |           |           |     |
|                                | 29                                    | 31 | 33 | 35 | 37 | 39 | 41 | 43 | 45 | 47 | 49 |           |           |           |           |     |
| <i>C. fischeri</i>             |                                       |    | 11 | 7  | 24 | 17 | 6  | 3  | —  | 2  |    |           |           | 70        | 37.0      | 3.1 |
| <i>C. hippos</i> (E. Atlantic) | 1                                     | 1  | 1  | 4  | 4  | 4  | 1  | 1  |    |    |    |           |           | 17        | 35.8      | 3.5 |
| <i>C. hippos</i> (W. Atlantic) | 1                                     | 2  | 10 | 18 | 17 | 18 | 12 | 3  | 1  |    |    |           |           | 82        | 36.7      | 3.1 |
| <i>C. caninus</i>              | 1                                     | —  | —  | 1  | 4  | 4  | 14 | 13 | 8  | 8  | 1  |           |           | 54        | 41.9      | 3.6 |

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**Table 4**  
Frequency distributions for gill raker counts in the *Caranx hippos* species complex.

| Upper limb gill rakers     |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
|----------------------------|-----------------|----|----|----|-----------|----|-----------|----|----|----|----|----|-----------------------------|----|-------|----|----|----|-----------|------|-----------|
| Species                    | Rudiments       |    |    |    |           |    | Developed |    |    |    |    |    |                             |    | Total |    |    |    |           |      | $\bar{x}$ |
|                            | 0               | 1  | 2  | 3  | 4         | 5  | 2         | 3  | 4  | 5  | 6  | 7  | 8                           | 4  | 5     | 6  | 7  | 8  | 9         |      |           |
| <i>C. fischeri</i>         |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 18              | 5  | —  | 1  | 1         |    |           | 1  | 1  | —  | 17 | 6  |                             |    |       | 13 | 11 | 1  |           | 6.5  |           |
| >10 cm FL                  | 9               | 13 | 7  | 10 | 6         |    |           | 3  | 14 | 7  | 4  | 16 | 1                           | 1  | 5     | 22 | 17 |    |           | 6.2  |           |
| <i>C. hippos</i> (E. Atl.) |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 8               | 12 | —  | 3  | 4         |    |           |    | 5  | 2  | 1  | 12 | 7                           |    |       | 4  | 21 | 2  |           | 6.9  |           |
| >10 cm FL                  |                 | 2  | 1  | 2  | 1         |    |           | 1  | 2  | —  | 2  | 1  |                             | 1  | —     | 2  | 2  | 1  |           | 6.8  |           |
| <i>C. hippos</i> (W. Atl.) |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 2               | 1  | —  | 1  | 1         |    |           |    | 2  | —  | —  | 1  | 2                           |    |       | 1  | 4  |    |           | 6.8  |           |
| >10 cm FL                  | 31              | 28 | 14 | 18 | 9         | 7  | 4         | 11 | 14 | 14 | 26 | 34 | 4                           |    |       | 10 | 63 | 34 |           | 7.2  |           |
| <i>C. caninus</i>          |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 9               | 2  | 1  |    |           |    |           |    |    |    | 1  | 5  | 6                           |    |       |    | 3  | 9  |           | 7.7  |           |
| >10 cm FL                  | 9               | 14 | 12 | 10 | 8         | 3  |           | 4  | 14 | 6  | 9  | 18 | 5                           |    |       | 1  | 16 | 36 | 3         | 7.7  |           |
| Lower limb gill rakers     |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| Species                    | Rudiments       |    |    |    | Developed |    |           |    |    |    |    |    | Total                       |    |       |    |    |    | $\bar{x}$ |      |           |
|                            | 0               | 1  | 2  | 3  | 13        | 14 | 15        | 16 | 17 | 18 | 16 | 17 | 18                          | 19 | 20    |    |    |    |           |      |           |
| <i>C. fischeri</i>         |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 4               | 11 | 10 |    |           | 3  | 11        | 7  | 4  |    |    | 7  | 18                          |    |       |    |    |    |           | 16.7 |           |
| >10 cm FL                  |                 | 2  | 35 | 8  |           | 14 | 26        | 5  |    |    |    | 10 | 28                          | 7  |       |    |    |    |           | 17.0 |           |
| <i>C. hippos</i> (E. Atl.) |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  |                 | 13 | 11 | 3  |           | 1  | 11        | 14 | 1  |    |    | 24 | 3                           |    |       |    |    |    |           | 16.1 |           |
| >10 cm FL                  |                 |    | 5  | 1  |           | 1  | 4         | 1  |    |    |    | 5  | 1                           |    |       |    |    |    |           | 16.2 |           |
| <i>C. hippos</i> (W. Atl.) |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  |                 | 1  | 2  | 2  |           |    | 2         | 2  | 1  |    |    | 1  | 3                           | 1  |       |    |    |    |           | 17.0 |           |
| >10 cm FL                  | 1               | 9  | 80 | 17 |           | 1  | 35        | 57 | 13 | 1  |    | 29 | 65                          | 13 |       |    |    |    |           | 16.9 |           |
| <i>C. caninus</i>          |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 4               | 8  |    |    |           |    |           |    | 2  | 6  | 4  |    | 3                           | 9  |       |    |    |    |           | 17.8 |           |
| >10 cm FL                  | 2               | 13 | 38 | 3  |           |    | 1         | 10 | 35 | 9  | 1  | 4  | 14                          | 31 | 6     | 1  |    |    |           | 17.8 |           |
| Total gill rakers          |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| Species                    | Total developed |    |    |    |           |    |           |    |    |    |    |    | Total developed + rudiments |    |       |    |    |    |           |      | $\bar{x}$ |
|                            | 16              | 17 | 18 | 19 | 20        | 21 | 22        | 23 | 24 | 25 | 26 | 20 | 21                          | 22 | 23    | 24 | 25 | 26 | 27        | 28   |           |
| <i>C. fischeri</i>         |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  |                 |    | 1  | 1  | —         | —  | 11        | 6  | 4  | 2  |    |    |                             | 5  | 10    | 10 |    |    |           | 23.2 |           |
| >10 cm FL                  | 2               | 6  | 13 | 4  | 5         | 11 | 3         | 1  |    |    |    | 2  | 2                           | 9  | 14    | 15 | 3  |    |           | 23.0 |           |
| <i>C. hippos</i> (E. Atl.) |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  |                 |    | 3  | 3  | 2         | 6  | 8         |    | 4  | 1  |    |    |                             | 4  | 21    | 2  |    |    |           | 23.0 |           |
| >10 cm FL                  | 1               | 2  | 1  | —  | 2         |    |           |    |    |    |    | 1  | —                           | 2  | 2     | —  | 1  |    |           | 22.5 |           |
| <i>C. hippos</i> (W. Atl.) |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  | 1               | 1  | —  | 1  | —         |    | 1         | 1  |    |    |    |    |                             | 2  | 3     |    |    |    |           | 23.6 |           |
| >10 cm FL                  | 4               | 6  | 11 | 14 | 12        | 25 | 25        | 9  | 1  |    |    |    |                             | 7  | 15    | 55 | 24 | 6  |           | 24.1 |           |
| <i>C. caninus</i>          |                 |    |    |    |           |    |           |    |    |    |    |    |                             |    |       |    |    |    |           |      |           |
| <10 cm FL                  |                 |    |    |    |           |    | 1         | 1  | 4  | 2  | 4  |    |                             |    | 2     | 2  | 8  |    |           | 25.5 |           |
| >10 cm FL                  |                 |    |    | 1  | 7         | 12 | 5         | 8  | 12 | 10 | 1  |    |                             |    | 2     | 7  | 19 | 21 | 6         | 1    | 25.4      |

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## Appendix 1

Catalog numbers, localities, and sizes (mm FL) of specimens used for outline drawings of the first dorsal-fin pterygiophore in Figure 11. Numbers in bold correspond to the numbers for the pterygiophores illustrated in Figure 11.

*Caranx caninus*: 1, ANSP 144406 (169) El Salvador; **2**, USNM 114469 (178) Guatemala; 3, USNM 820080 (187) Panama; 4, USNM 47145 Gulf of California (192); 5, USNM 114469 Guatemala (197); **6**, CAS 66938 Ecuador (212); 7, USNM 47144 Gulf of California (213); 8, ANSP 144401 El Salvador (220); **9**, USNM 114469 Guatemala (227); **10**, USNM 114469 Guatemala (233); **11**, USNM 200728 El Salvador (240); **12**, ANSP 158506 Mexico, Sinaloa (248); **13**, ANSP 158506 Mexico, Sinaloa (258); **14**, USNM 101006 Mexico (261); **15**, ANSP 158506 Mexico, Sinaloa (262); **16**, USNM 28293 Mexico (304); **17**, USNM 205166 Baja California (307); **18**, ANSP 158506 Mexico, Sinaloa (313); **19**, CAS 42539 3°53'N, 105°10'W (333); **20**, CAS 11112 Mexico (329); **21**, US-



NM 79884 Panama (348); **22**, USNM 127918 Peru (359); **23**, USNM 127919 Peru (360); **24**, SIO 62-61 Mexico, Isabel Island (371); **25**, USNM 100991 Mexico (381); **26**, USNM 100998 Mexico (399); **27**, SIO 62-61 Mexico, Isabel Island (419); **28**, CAS 216872 Baja California (421); **29**, SIO 65-182 (431); **30**, SIO-62-61 Mexico, Isabel Island (438); **31**, USNM 206999 Colombia (490); **32**, USNM 128659 Panama (520); **33**, CAS 216871 Tres Marias Island (538); **34**, SIO 58-83 Peru (588); **35**, SIO 75-383 California, San Diego (643); **36**, SIO 65-176A Baja California (670).

*Caranx hippos*: **37**, USNM 57294 (176) Florida; **38**, ANSP 97864 (176) New Jersey; **39**, ANSP 97864 (189) New Jersey; **40**, ANSP 151093 (198) Florida; **41**, USNM 121801 (205); Venezuela **42**, ANSP 151093 Florida (207); **43**, USNM 121801 (213) Venezuela; **44**, CAS 122133 (223) Brazil; **45**, CAS 122133 (228) Brazil; **46**, ANSP 158504 (233) Honduras; **47**, CAS 122133 (235) Brazil; **48**, ANSP 151589 (254) Puerto Rico; **49**, ANSP 158504 (251) Honduras; **50**, USNM 12681 (254) Key West; **51**, USNM 12681 (269) Key West; **52**, AMNH 3889 (274) Brazil; **53**, ANSP 148238 (294) French Guiana; **54**, ANSP 102112 (298) Brazil; **55**, AMNH 3889 (300) Brazil; **56**, CAS 153016 (316) Brazil; **57**, CAS 153016 (319) Brazil; **58**, USNM 114618 (326) Guatemala; **59**, USNM 114618 (332) Guatemala; **60**, USNM 128658 (334) Panama; **61**, USNM 128658 (350) Panama; **62**, USNM 114618 (360) Guatemala; **63**, USNM 128657 (364) Panama; **64**, ANSP 93821 (366) Florida; **65**, USNM 29986 (372) Rhode Island; **66**, USNM 19821 (386) Cuba; **67**, USNM 132964 (400) Cuba; **68**, USNM 114594 (420) Guatemala; **69**, USNM 332457 (421) Florida; **70**, USNM 362541 (430) Florida; **71**, USNM 79981 Panama (440); **72**, USNM 362541 (460) Florida; **73**, USNM 362541 (470) Florida; **74**, USNM 114816 (485) Guatemala; **75**, CAS 153082 (534) Brazil; **76**, CAS 153082 (555) Brazil; **77**, CAS 153080 (605) Brazil; **78**, CAS 153080 (617) Brazil; **79**, USNM 22855 Gulf of Mexico (622); **80**, ANSP 159674 (655) Mexico; **81**, ANSP 102762 (657) Bahamas; **82**, USNM 32080 (725) Jamaica; **83**, CAS 216873 (1015) Florida; **84**, MNHN 1978-230 (274) "tropical West Africa"; **85**, MNHN 1978-216 (331) Western Sahara; **86**, ZMUC 25 (565) Senegal, Dakar; **87**, USNM 377462 (1070 estimated, 130 cm TL measured), Guinea-Bissau.

*Caranx fischeri*: **88**, CAS 38375 (159) Nigeria; **89**, USNM 27566 (163) Sierra Leone; **90**, CAS-SU 15885 (171) Cameroon; **91**, ANSP 158493 (173) Gulf of Guinea, Bioko; **92**, ANSP 158493 (182) Bioko; **93**, ANSP 158493 (197) Bioko; **94**, USNM 279566 (203) Sierra Leone; **95**, ANSP 158497 (237) Sierra Leone; **96**, ANSP 158498 (239) Sierra Leone; **97**, BMNH 1939.7.12.12 (271) Gold Coast; **98**, MNHN 1978-260 (313) Senegal; **99**, MNHN 1978-235 (317) "tropical West Africa"; **100**, ANSP 140256 (328) Cameroon; **101**, BMNH 1899.11.27.87 (348) Congo; **102**, BMNH 1927.12.7.49 (358) Ascension Island; **103**, MRAC 87428 (367) Congo; **104**, MRAC 36 (403) Congo; **105**, ZMUC P.46362 (450) Nigeria; **106**, IRSNB 829 (530) Senegal.

## Appendix 2

Catalog numbers, localities, and sizes (mm FL) of specimens used for the outline drawings of the eighth precaudal vertebra in Figure 13. Number in bold correspond to the numbers for the vertebrae illustrated in Figure 13.

*Caranx hippos*: **1**, USNM 19821 (357), Cuba; **2**, USNM 114618 (360), Guatemala; **3**, USNM (400) Cuba; **4**, USNM 11490 (420) Guatemala; **5**, USNM 3324557 (421) Florida, Swanee River; **6**, USNM 79981 (440), Panama, Colon; **7**, USNM 362541 (470), Florida, Caloosahatchee River; **8**, USNM 115618 (485), Guatemala; **9**, CAS-SU (534) Brazil; **10**, CAS-SU 53082 (555) Brazil; **11**, USNM 114618 (557) Guatemala; **12**, CAS-SU 53080 (605) Brazil; **13**, USNM 22855 (622) Florida, Pensacola; **14**, ANSP 159674 (655) Mexico, Carmen; **15**, ANSP 102762 (657) Bahamas, Andros Island; **16**, ANSP 159674 (698) Mexico, Carmen; **17**, ANSP 159674 (717) Mexico, Carmen; **18**, ZMUC (565) Senegal, Dakar

*Caranx caninus*: **19**, USNM 127918 (359) Peru, Lobos de Tierra; **20**, SIO-62-61 (371) Mexico, Isabel Island; **21**, USNM 10099 (381), Mexico, Petarabo Bay; **22**, USNM 100998 (399) Mexico; **23**, SIO 62-61 (419) Mexico, Isabel Id.; **24**, SIO 65-182 (431) Mexico, Baja; **25**, USNM 206999 (490) Colombia, Baja Utria; **26**, USNM 128659 (520) Panama, Miraflores Lock; **27**, CAS 216871 (538) Tres Marias Is.; **28**, SIO 58-83 (588) Peru; **29**, SIO 75-383 (643), San Diego Bay; **30**, SIO 65-176A (670), Baja California.

## Appendix 3

Catalog numbers, localities, and sizes (mm FL) of specimens used for the outline drawings of the first anal-fin pterygiophore in Figure 15. Numbers in bold font correspond to the numbers for the pterygiophores seen in Figure 15.

*Caranx caninus*: **1**, SIO-62-61 (419) Mexico, Isabel Island; **2**, CAS 216872 (421) Baja California; **3**, SIO-62-61 (438) Mexico, Isabel Island; **4**, USNM 206999 (490) Colombia; **5**, CAS 21871(538) Tres Marias Island; **6**, SIO 58-83 (588) Peru; **7**, SIO 75-383 (643) California, San Diego; **8**, SIO 65-176A (670) Baja California.

*Caranx hippos*: **9**, USNM 114594 (420) Guatemala; **10**, USNM 79981 (440) Panama, Colon; **11**, USNM 362541 (460) Florida, Caloosahatchee River; **12**, USNM 362541 (470), Florida, Caloosahatchee River; **13**, USNM 114618 (485) Guatemala; **14**, CAS-SU 53082 (534) Brazil; **15**, CAS-SU 53082 (534) Brazil; **16**, USNM 114618 (557), Guatemala; **17**, CAS-SU 53082 (555) Brazil; **18**, CAS-SU 53080 (617) Brazil; **19**, ANSP 159674 (655) Mexico; **20**, ANSP 102762 (657) Bahamas; **21**, ANSP 159674 (698) Mexico.